EAST AFRICAN MAMMALS

An Atlas of Evolution in Africa

Volume IIIB

Jonathan Kingdon

Academic Press
London New York San Francisco
A Subsidiary of Harcourt Brace Jovanovich, Publishers

Naturalists will have been waiting eagerly for this penultimate part to the third volume of Jonathan Kingdon's treatise, *East African Mammals*. His extraordinary drawings that reveal fine structural and anatomical details with such clarity, and the dedication and thoroughness with which the text of earlier volumes was invested have earned international acclaim. As a *tour de force* of artistic and scientific merit there can be few comparisons in its field.

Part B of the third volume moves on from the carnivores of Part A to the large mammals for which Africa is so famous: the elephants, rhinos, the equids including the strange Painted Quagga, the pigs, the hippopotamuses, the camels, the chevrotains and giraffes. Broadly, it sets out to portray the role of these beautiful animals in tropical Africa's ecology and the evolutionary and functional significance of their curious forms and markings. The searching text is enhanced throughout, as in earlier volumes, by the author's exquisite drawings and sketches. Their adaptive morphology is seen in the context of behaviour and ecology and in the light shed by the evidence from fossils found during the last decade. Original contributions are made to the morphological study of elephants, suids and perissodactyls while such old questions as the striping of zebras, the warts of warthogs and the blotchings of giraffes are discussed afresh with much new information on the biology of giant hogs and the hippopotamus.

As in all the previous volumes of *East African Mammals*, Jonathan Kingdon's approach is uniquely broad in its appeal. Primarily its success is a scientific one: our knowledge of the biology of African fauna is infused with the author's original contributions and strengthened by the updating of established texts. New data on the zoogeography of the continent and an overall ecological perspective broaden the scope of his work while the author's intricate illustrations bring to the text a visual complement of outstanding beauty. The book countenances the inevitable problems posed by large mammal communities in a developing continent and numerous maps indicate their declining populations. While it is sadly necessary to include such information in a book of this nature, it is to be hoped that from it will spring a greater understanding of the need for a conservationist approach in all our dealings with African wild life.

"*No naturalist, nor anyone else connected with East Africa's wildlife can afford to be without this magnificent and monumental work. When all three volumes are out the layman will at long last be in the happy position of being able to identify any East African mammal . . . as well as gaining a considerable insight into its habits and evolutionary background.*"

Bulletin of the East Africa Natural History Society

£98·00

Donat Agosti
Vi. 90
London

EAST
AFRICAN MAMMALS

Jonathan Kingdon

EAST AFRICAN MAMMALS

An Atlas of Evolution in Africa

Volume III Part B (Large Mammals)

1979

Academic Press London New York San Francisco

Subsidiary of Harcourt Brace Jovanovich, Publishers

ACADEMIC PRESS INC. (LONDON) LTD
24–28 Oval Road
London, NW1

U.S. Edition published by
ACADEMIC PRESS INC.
111 Fifth Avenue
New York, New York 10003

Kingdon, Jonathan
East African mammals.
Vol. III. Part B: Large mammals
1. Mammals—Africa, East
I. Title
599′.0967 QL731.A32 73–117136

ISBN 0–12–408343–9

PRINTED IN GREAT BRITAIN BY
WILLIAM CLOWES (BECCLES) LIMITED, BECCLES AND LONDON

Contents

INTRODUCTION LARGE MAMMALS	1
PROBOSCIDS (Proboscidea)	8
ELEPHANTIDS (Elephantidae)	18
Elephant, *Loxodonta africana*	30
PERISSODACTYLS (Perissodactyla)	76
CERATOMORPHS (Ceratomorpha) etc	80
Black rhinoceros, Browse rhinoceros, *Diceros bicornis*	92
White rhinoceros, Grass rhinoceros, *Ceratotherium simum*	106
EQUIDS (Equidae)	120
Horses, Zebras and Asses, *Equus*	125
Grevy's zebra, Somali zebra, *Equus grevyi*	146
Ass, Donkey, *Equus asinus* (no text)	162
Horse, Pony, *Equus caballus* (no text)	162
Common zebra, Painted quagga, *Equus quagga*	163
ARTIODACTYLS (Artiodactyla)	180
PIGS (Suidae)	184
Bushpig, River hog, *Potamochoerus porcus*	200
Giant hog, *Hylochoerus meinertzhageni*	210
Warthog, *Phacochoerus aethiopicus*	230
HIPPOPOTAMIDS (Hippopotamidae)	250
Hippopotamus, Hippo, *Hippopotamus amphibius*	256
TYLOPODA	278
CAMELS (Camelidae)	278
Camel, Dromedary, *Camelus dromedarius*	280
CHEVROTAINS (Tragulidae)	295
Water chevrotain, *Hyemoschus aquaticus*	298
GIRAFFIDS (Giraffidae)	308
Giraffe, *Giraffa camelopardalis*	312
Okapi, *Okapia johnstoni*	338
APPENDIX	346
BIBLIOGRAPHY	347
SYSTEMATIC INDEX	411
SUBJECT INDEX	417

Introduction

Large Mammals

There is a school of ecologists that, making the best of the world as they find it, assert that rats can be just as interesting as elephants. This may be true, yet the human animal within the naturalist still finds himself gripped by an excited interest in those animals that are bigger than himself, particularly if he is without the protection of arms or a vehicle.

Perhaps it was the intrusion of just such subjective and personal feelings that helped delay scientific study of large mammals in their natural environments to the point where it was almost too late. Large mammals have long lives and their impact on the environment, particularly when they exist in large numbers, introduces complex long-term changes of which we know very little. All recent students of large mammals and of their tropical environments have lamented the shallow dimension of time in their studies.

An awareness of such areas of ignorance must continue to qualify our investigation of the roles of animals and plants within their ecological communities and temper our excitement as we reveal more precisely the niches of living animals in contemporary ecosystems.

It is not just knowledge and historical data that are missing, it is actual species of large mammals. Without exception the large mammals of today belong to simpler communities and in most cases fill broader niches than they evolved to occupy. Until very late in the Pleistocene there were several elephant species, several hippopotamuses, four or five giraffes, an abundance of giant pigs and there were enigmatic giants such as the perissodactyl chalicothere.

While earlier volumes have dealt with well defined and relatively homogeneous Orders, the common denominator for the species described in Volume IIIB is that they are of large size (excepting the chevrotain). It must be recognized that it is difficult to put across some of the implications of scale in a book that allots equal space to the dissection of a shrew and a hippopotamus yet size has a number of implications for the natural history of these animals. Some of the more general of these can be touched on here while more specific topics are discussed in the profiles of species.

Because these mammals are bigger than us and need more room than us our immediate interest must be a concern for their survival within their natural environment. All the species described in this part of Volume III are in a decline that has accelerated in recent years and can only continue. Not only are the animals desirable as meat or trophies, they are increasingly accessible and the land they use will beckon with ever increasing urgency to would-be colonists with new techniques to tame the soil.

Among the implications of this volume there is the insistent reminder that we are in danger of diminishing the scale of the natural world, reducing it to the miserable dimensions of temporary human enterprises. We are in danger of losing diversity and contrast and we are congenitally hell-bent on simplifying natural complexity even while we elaborate our own rituals and inventions. Our civilization is speeding up the turnover of its technology so that the inventions of today will be irrelevant tomorrow; at the same time the natural world has been swept up into this ever faster cycle of redundancies. In the mythology of our times the remaining large mammals are intrinsically as redundant as the legions of extinct giants that preceded them or the quaint inventions of our fathers: they share cases in the museum. In practice, however, the equation is a simple one, the large mammals are still our biological competitors and they, together with the forests and savannas must make way for more coffee, tea, sugar and bread for the world's breakfast tables. It has been suggested that the large animals might be best conserved by themselves appearing on the table.

There has been considerable interest in the exploitation of large mammals for meat. It is true that elephants, hippo and zebra have some potential but in spite of being relatively modest consumers all the large mammals have a low rate of turnover because of the many years taken to reach maturity. In a cost-conscious world, protein production is an inadequate rationale for the preservation of individual species. In this limited context the choice is sometimes presented as semi-domestication versus extinction. This topic will be discussed at greater length in relation to the bovids but the obvious conclusion is that large mammals are part of a very complex community in which a great many organisms are interacting. Very considerable areas of land are required for the survival of such eco-systems but their overall production may also be very high and the feasibility of cropping a variety of species within National Parks and Sanctuaries or in zones surrounding them has been proven. However, it should always be recognized that this production is essentially a by-product or bonus subsidiary to our primary responsibility for preserving this fauna and flora intact.

It was mentioned above that the contemporary large mammals are the survivors of formerly more diverse communities of large mammals. These survivors are versatile species with sufficient ecological plasticity to adapt to changes in their habitat and it seems to be this that distinguishes them from most of their extinct relatives, some of which were more highly specialized.

Why were the specialists vulnerable? In the first place very large vegetarians can only afford to be selective in a rich and relatively stable habitat and cannot easily adapt to major fluctuations in their food supply. Changes such as those wrought by increasingly widespread use of fire by early man could therefore have been a major factor in the extinction of some very large herbivores.

In any competitive situation a specialist tends to be less adaptable, even to relatively minor changes in the pattern of climate and vegetation so that the contemporary survivors might have hastened the extinction of their relatives by competing with them and progressively narrowing their ecological niche.

Ecological specialization is often associated with elaboration of the social system. In large mammals socialization is generally linked with a long period of learning or a relatively slow, staged progression towards adulthood and reproductive status, thereby slowing down an already slow turnover rate. (Indeed, in terms of bioenergetics the evolution of large size can be described as a mechanism to slow down energy flow.) The benefits of a leisurely infancy and adolescence tend to be reduced under unstable conditions and it is conceivable that some extinct mammals were peculiarly reliant upon the maintenance of elaborate social systems which in turn depended for their development on a long period of learning.

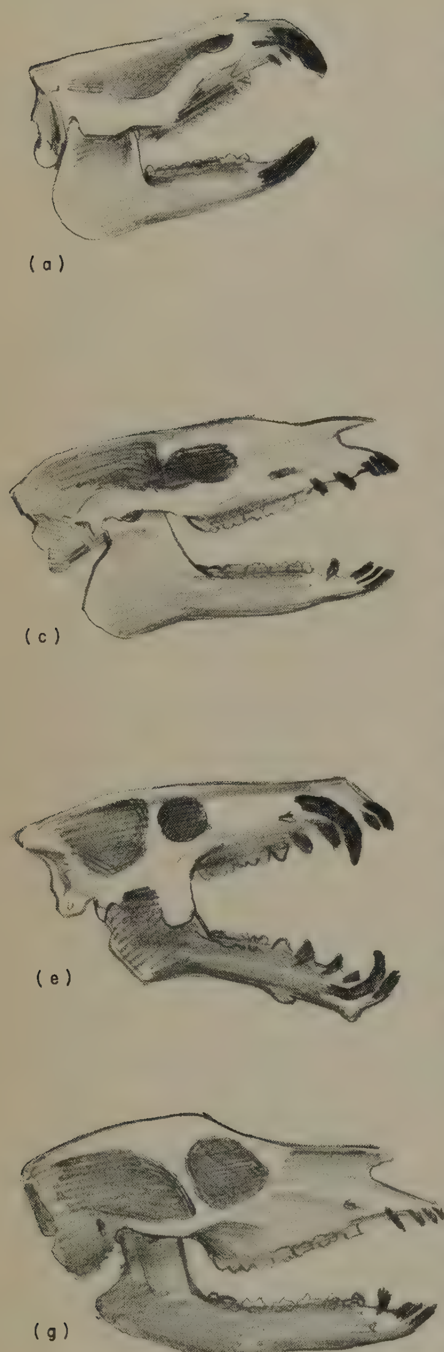
The implications of impending extinction for several species give a special urgency to studies of social development and individual maturation, yet it would require half a lifetime to study this process in an elephant and undisturbed elephant populations are increasingly rare even in national parks.

The profile on elephants describes some of the situations created by the impact of great numbers of large mammals in limited areas. The novelty of the situation in Tsavo National Park may be appreciated when it is remembered that this artificially constricted population was consuming large numbers of very large baobabs, trees which have been aged elsewhere by radiocarbon dating from 1,000 to over 5,000 years old (Swart, 1963).

Formerly academic topics concerning the regulation of animal numbers have acquired highly controversial and practical connotations in the National Parks of East Africa. Opponents of any form of management or interference in these sanctuaries would cite Wynne Edwards (1962) who thought that populations were ultimately self-regulating through the evolution of various behavioural mechanisms that have been evolved to this end. Or else they followed Andrewartha and Birch (1954) in believing that numbers were controlled independently of density. In practice, populations of large mammals, particularly elephants and rhinoceroses in Tsavo, seem to have been limited by a shortage of food and water that was directly dependent upon artificially high densities. Starvation was augmented by disease confirming Nicholson's (1933) Darwinian stress on food, predation and disease as the ultimate regulators of numbers.

In the Tsavo situation rhinos starved in large numbers because a larger animal consumed a food supply that was normally very abundant and reliable. Elsewhere large mammals have suffered from more efficient or more numerous competitors but the rapid decline of formerly successful species can be attributed to a new voracious predator penetrating their defences. One implication of this vulnerability is that some species may have passed through an evolutionary stage of living within habitats with very abundant food where they could feed and breed with security from predation. Ancestral forms living in swamps or thickets might have achieved there the size and hence the relative invulnerability to emerge into more exposed habitats.

Phylogenetic shifts from one ecological niche into another have almost endless implications (and give a special interest to the two rhinoceros species). Where the distribution of food changes, the spatial pattern of individuals and classes must alter. This in turn can put demands on many aspects of behaviour including the breeding strategy and may lead to new permutations in established repertoires and complicated changes in the social system.



(a) *Moeritherium* (Eocene paenungulate); (c) *Hyracotherium* (Eocene perissodactyl); (e) *Archaeotherium* (Oligocene suine); (g) *Archaeomeryx* (Eocene pecoran).

Physiology must adjust to such changes and increasing size combines with environmental alterations to influence many physiological parameters, for example, temperature regulation.

With the exception of the camel and to a lesser extent the giraffe, large mammals need to drink regularly. Large bodies tend to overheat and both pachyderms and the diurnal warthogs have problems in regulating their body temperature which they solve by wallowing. Water in mud continues to evaporate for over an hour and these animals cool themselves during the middle of the day, during the dry season, by seeking out wallows. Both behaviour and skin seem to have adapted to use this property of mud.

Digestive efficiency, activity cycles and behaviour have considerable relevance for the relationship between an animal's size and its food supply and other environmental checks may put tight upper limits on size but the assumption that there is a close correlation between size and the amount of food eaten and between size and the abundance of resources is not borne out by the facts. Some relatively small animals eat as much as very large ones and many large mammals are unable to depend upon locally concentrated food supplies. Intraspecific competition is probably a more important factor in determining size. Trials of strength are very often trials of relative bulk or weight so that many already large mammals are subject to continuous selection in favour of still greater bulk, particularly among males. The lifting of such environmental checks during very favourable periods might explain those Pleistocene eras when gigantism was prevalent in many mammal lineages.

Virtually all mammals compete or fight among themselves. In small mammals relatively inconspicuous teeth or claws serve this purpose. However, large mammals generally need large weapons and it is for this reason that elephant, rhinoceros pigs, hippopotamus and other artiodactyls have, throughout their evolutionary history, nearly always been equipped with a variety of horns, tusks and teeth which are a conspicuous and integral part of their anatomy.

There is a relationship between increasing intraspecific contacts or population density and the ritualization of fighting. Animals that possess dangerous weapons and yet fight without such constraints can avoid frequent repetition of these dangerous encounters by spacing themselves far apart. In any case the severity of their fights tends to bring about this state of affairs with the result that the species is likely to fall far short of exploiting its habitat's potential carrying capacity. The dangers of confrontation may also inhibit or impair reproductive efficiency.

Within a broad phylogenetic perspective it is likely that "avoiders" with attenuated social contacts might have reduced the chances of developing more effective ways of exploiting the environment by evolving different modes of dispersal. The morphology and social behaviour of the chevrotain suggest that this primitive sabre-toothed ungulate has been trapped in just such an evolutionary backwater (see pp. 294 *et seq.*).

Our understanding of a species' evolution, of its physical shape and of its biology is incomplete unless we recognize the importance of intraspecific competition and examine its role within the life of each species for it is in the

shapes and proportions of their weapons that many mammals differ most, and this diversity has a relatively simple evolutionary explanation.

In terms of natural selection and survival "winning the battle does not necessarily win the war" and successfully holding off a rival is as significant as wounding or killing him. When one animal succeeds in preventing another from using its weapons its defensive strategy and the physical equipment that contribute to a successful defence have a positive survival value. A predator's weapons are of such critical importance for catching food that they generally cannot be modified for use against conspecifics and it is only behaviour that can be differentiated.

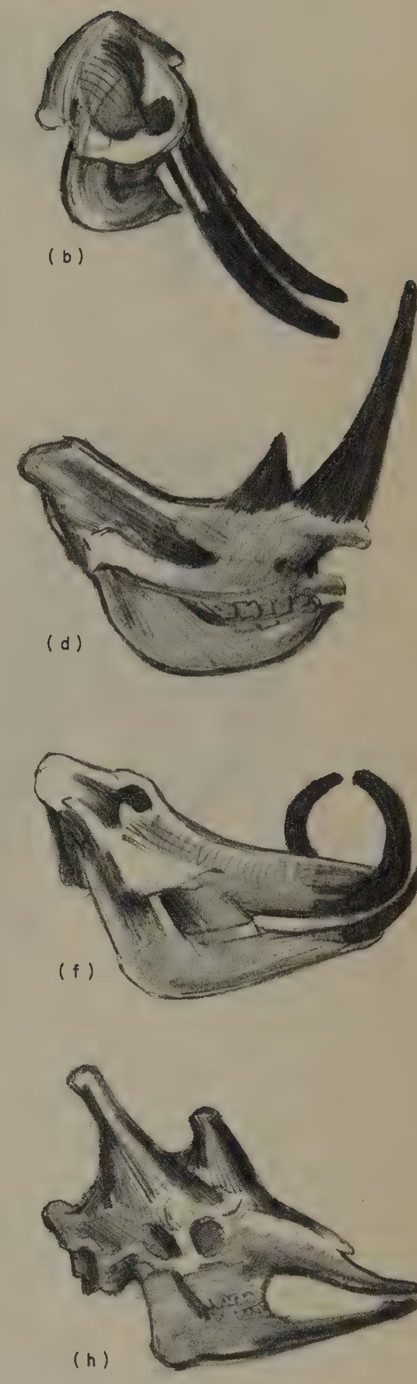
Animals that are not predatory lack this constraint, so both behaviour and weaponry can be differentiated and where other defences such as flight, concealment or great size are available weaponry is directed towards intraspecific competition. Even in the instances where attack or defence against other species assists survival it is usually inappropriate to use the same weapons because a rival of the same species matches his opponent feature for feature.

There is a direct relationship between the shape of a weapon and the devices and manoeuvres that counteract it. Since both contestants must continually switch from attack to defence the physical equipment serving these ends must be physically close or contiguous and most horns and tusks etc. combine offensive and defensive zones within a single structure.

The defensive components of fighting are especially significant because it is only an effective defence that maintains an engagement. Once these are breached the contest is generally settled so that an animal's physiology and anatomy must contend with the expenditure of much time and energy in mutual sparring. The movements and physical adaptations that originally parried or fended off an onslaught therefore acquire an autonomy of their own and it is important to recognize that defensive behaviour can become ritualized to the point where antagonists hardly ever employ the offensive weapons or movements that their sparring was designed to neutralize.

This development can be illustrated by reference to the pigs. The earliest suids were probably predatory and retained functional canines. Later, as they became more omnivorous the canines changed their orientation and flared out sideways. The lower canine retained a very sharp cutting edge and sharp point and has remained an important weapon in virtually all pigs up to the present. The upper tooth acts as a hone for the lower and in its primitive condition might have been useful for loosening the soil but in any dangerous encounter between pigs the upper canine probably served to contain or deflect an adversary's slashes.

In the warthog, the upper canines have become "snout antlers" and the functions of the upper and lower canines are clearly distinct. The lower are reserved for slashing at predators and are very seldom used against another pig. The upper not only function as a defensive barrier but defensive parrying seems to have been ritualized to the point where these movements rather than the dangerous slash have become the offensive element in intraspecific fighting. These heavy blunt tusks, therefore, deliver hammer-like blows as well as absorb them, they are also used as locking devices for pushing contests (see p. 233).



(b) *Loxodonta*: elephant; (d) *Ceratotherium*: grass rhino; (f) *Phacochoerus*: warthog; (h) *Giraffa*: giraffe.

The ritualization of defensive movements has followed a completely different course in the hippopotamus but parrying with open jaws has been ritualized into jaw clashing in which the incisors and canines act in a manner analogous to antler tines. This animal seems to be specially adapted to withstand the severe wounding that occurs whenever open-jawed bites are not parried (see p. 259).

Most large mammals concentrate their weapons in the head because a heavy body demands legs that have a more strictly supportive function. These weapons are of crucial importance in the biology of large mammals in determining stable hierarchies or territorial claims. They are amongst the most fascinating structures that distinguish one species from another and there is great interest in attempting to trace the hidden evolutionary changes and sequences that are behind the external shapes of horns and tusks, the processes of ritualization and the phylogenetic evolution of particular fighting patterns.

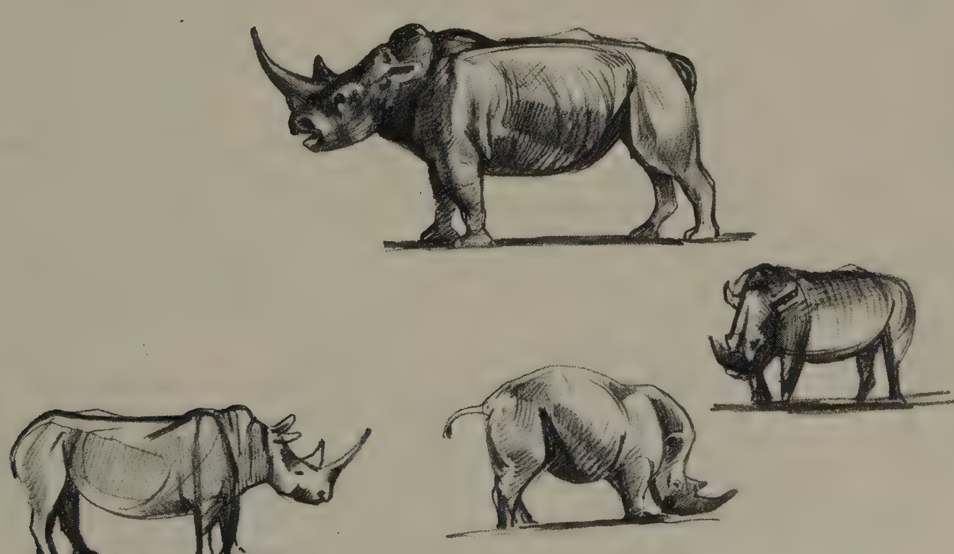
Many large animals not only employ horns or tusks against rivals—they thrash bushes, push trees or horn the ground. This tends to be commonest in immature males. When it takes place in the presence of a larger male it is

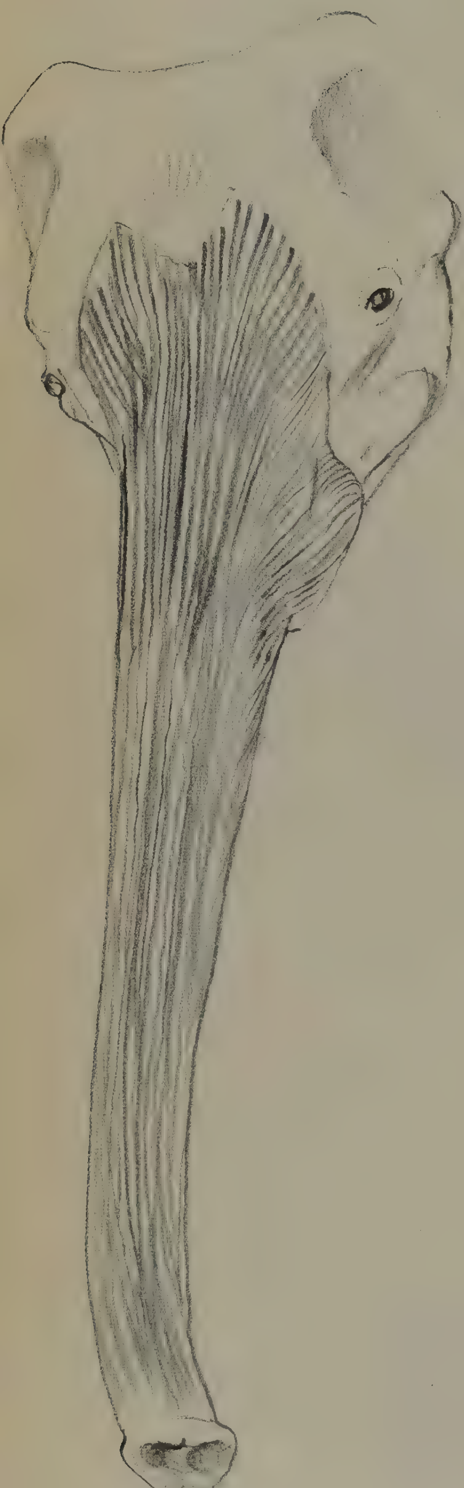
often interpreted as redirected aggression. In the absence of a rival, it may have the character of a sudden internally triggered impulse and it is common for elements of apparently innate behaviour that belong to disciplined adult repertoires to appear out of context in young and inexperienced animals.

However, infantile behaviours are not only a prelude to adult life but they sometimes provide a basis for important advances in social adaptation. For example, it has been shown (Volume IIIA) how the extension into adult life of *Lycaon* puppies' food-begging serves important social ends, and social adaptation in many species, notably zebras (p. 134) may depend upon the carry-over of juvenile behaviour into adult life. Display and ritualized combat may also include elements derived from youthful play-like experiments and the investigation of all types of social interaction in large mammals is a promising field of future study.

The study and conservation of large mammals in the wild is being pursued more seriously today than ever before and we owe a deeper appreciation and understanding of these animals to several outstanding students of their ecology and behaviour. In the profiles that follow, the work of these pioneers have provided a variety of topics for discussion, kaleidoscopic viewpoints of the animals and their biology. A contemporary observer must repeatedly overhaul his ideas and each perspective involves a different mode of thinking. Yet comprehending the evolutionary process remains the primary goal of these studies and of this book.

I have admitted (in Volume I) to a curiosity about form, particularly the impressive architecture of large mammals, being an incentive for the preparation of this book. On a human scale elephants, giraffes and rhinos are truly monumental but in a Malthusian world what are they monuments to, if not their own redundancy? No, they are imposing monuments to the process that evolved them—they are a challenge to our understanding and to an imagination that is increasingly conditioned by scientific knowledge.





Proboscids

Proboscidea

To a human the elephant is one of the most impressive animals on earth and its extraordinary and gigantic architecture illustrates the importance of viewing animals in the evolutionary dimensions of time and seeing their form in functional terms.

Many of the peculiar features of the elephant's body architecture and physiology are ingenious mechanical and biochemical solutions to problems that have been posed by enormous size, height and by a long life.

Increasing the weight and lengthening the life have demanded fundamental changes in apparently simple activities such as walking, feeding, drinking, fighting and reproduction.

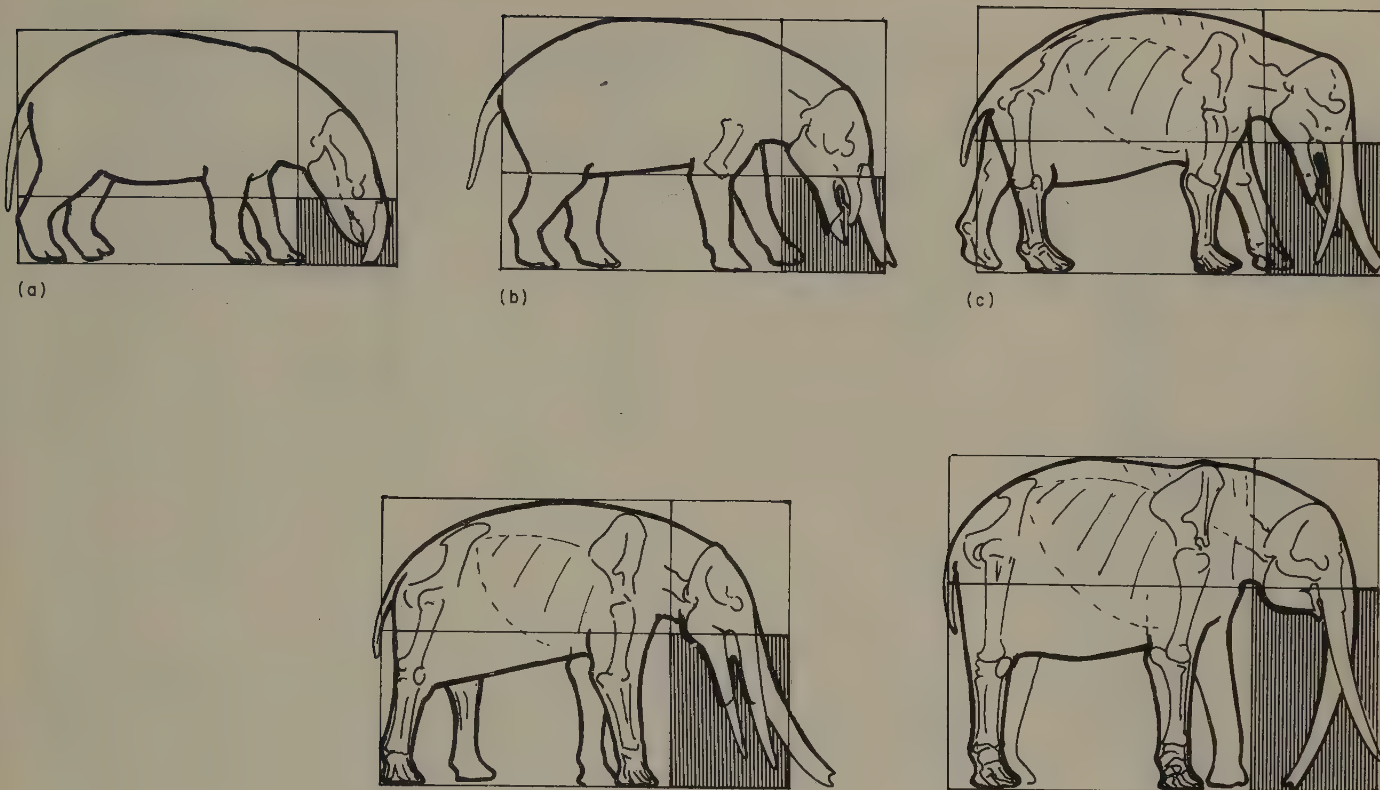
The Order gets its name from that most remarkable structure, the trunk. This derived in the very earliest ancestral proboscid from muscles surrounding the nostrils and serving the upper lip. Possession of a short food-gathering proboscis was probably an essential precondition for later developments and primitive proboscids must have resembled modern tapirs with tubby figures and mobile trunk. Indeed, they also may have lived in swamp forest or riverine habitats and filled similar or identical niches (which may be one reason for the total absence of tapirs, both fossil and living, in Africa).

The origin of the trunk was explained by Gregory (1903) as a response to "the shortening reach of the head and neck which took place simultaneously with increasing stature and longer limbs, partly to the necessity of reaching outside the lengthening tusks, partly to the intrinsic advantages of a prehensile organ of such manifold possibilities."

The intrinsic advantages of a proboscis are quite enough to explain its development, and increasing height and development of tusks may in fact be consequent upon the possession of a trunk and may be made possible because of it. It is certainly unnecessary to invoke tallness to explain a tapir's trunk.

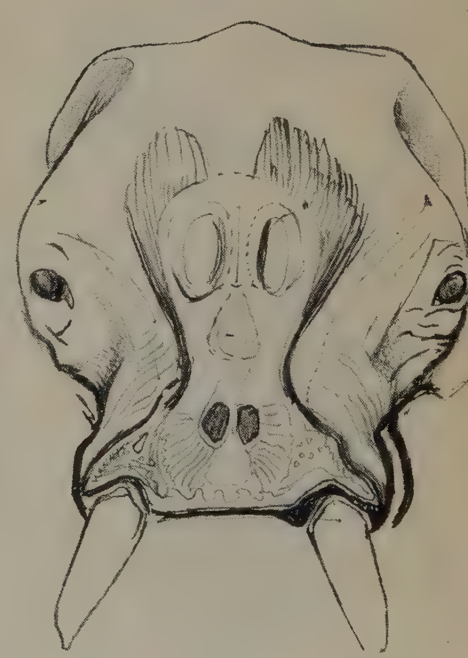
It has been argued by several authors that progressive lengthening of the mandibles and incisors in the earlier proboscis was concomitant with keeping the mouth in contact with the ground without lengthening the neck and that the length compensated for increasing height (Spinage, 1972b). In some specialized species the incisor teeth of either upper or lower jaw, or both, might have assisted in loosening or scooping up food, particularly the more primitive forms, but for the majority their role in feeding surely diminished as the diastema with the molars widened. As the distance increased between the grinding cheek teeth and standing food plants, the trunk must have been both gatherer and vehicle for all food irrespective of the extent to which tusks came into contact with the vegetation. As the elephants became taller, so must their trunks have become longer.

The modern elephant has an extensible tube of muscle fibres arising from the frontal maxillary and intermaxillary bones. The *maxillo-labialis* muscle runs the full length of the trunk and is in two parts, allowing contraction and expansion of the outer (upper) surface or of the inner (lower) surface. The superior part arises from the frontal and maxillary bones in the region between the eyes and it follows the cylindrical profile of the trunk's tube.



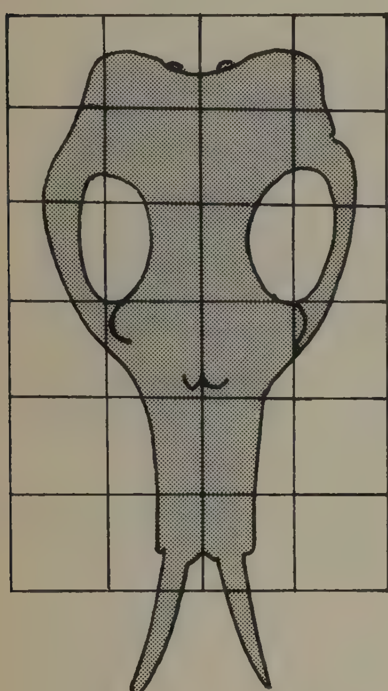
Changes of proportions in the evolution of Elephants. Horizontal line indicates rising level of mouth. Texture indicates principal feeding zone. (a) Reconstruction of ancestral proboscid (b) *Phiomia* (c) *Gomphotherium* (d) *Stegotetrabelodon* (e) *Loxodonta africana*.

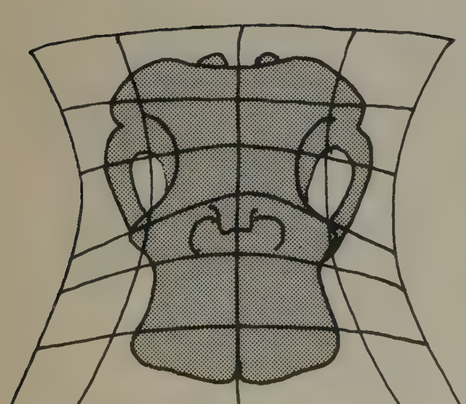
The inferior part arises from the lower corners of the maxilla, has great contractile strength and the profile of this muscle surface is flat, permitting the trunk to coil tightly. The two parts of the maxillo-labialis are fused to form a long tube within which the *m. rectus nasi* radiates out from the circumference of the nasal tubes right up to the intermaxillary bones. From the nasal cavity, *m. lateralis nasi* inserts into the mucous membrane of the nose. *Pyramidalis* and *orbicularis oris* muscles are incorporated in the upper regions.



The trunk is capable of powerful twisting and coiling actions in the course of gathering food or in wrestling bouts but it also performs delicate movements such as picking berries, rubbing an eye or exploring an orifice. A column of water or dust can be drawn up the trunk and squirted out again and the lungs adhere to the walls of the thoracic cavity to sustain the suction involved in this activity. The trunk increases the elephant's capabilities in various ways. It means it can reach to a height of up to 7 m and also excavate and dig down deep into sand or mud to reach water, allowing elephants to live in otherwise waterless regions. As Laws (1970b) has remarked, the trunk is typically invertebrate in its structure and mechanics and immense problems must have been posed in developing a precise manipulative organ to this specification. Its motor and sensory mechanisms await full investigation.

Changing proportions in the Proboscid skull. Above: *Phiomia* (Lower Oligocene); Below: *Loxodonta*.





While the development of a muscular trunk relieved the incisor teeth of their feeding function, progressive increases in size must have enhanced their importance as weapons in intraspecific competition. Great size reduces the versatility of limbs because their function is limited to weight bearing and leverage, so that the animal's physical contacts with its fellows and with its environment become very largely concentrated in the head. The trunk handles food and conducts some gentler forms of intraspecific contact but proboscids have not been unusual in employing their teeth as weapons against conspecifics and they have been typical in ritualizing fighting behaviour so that the dangers of conflict are reduced.

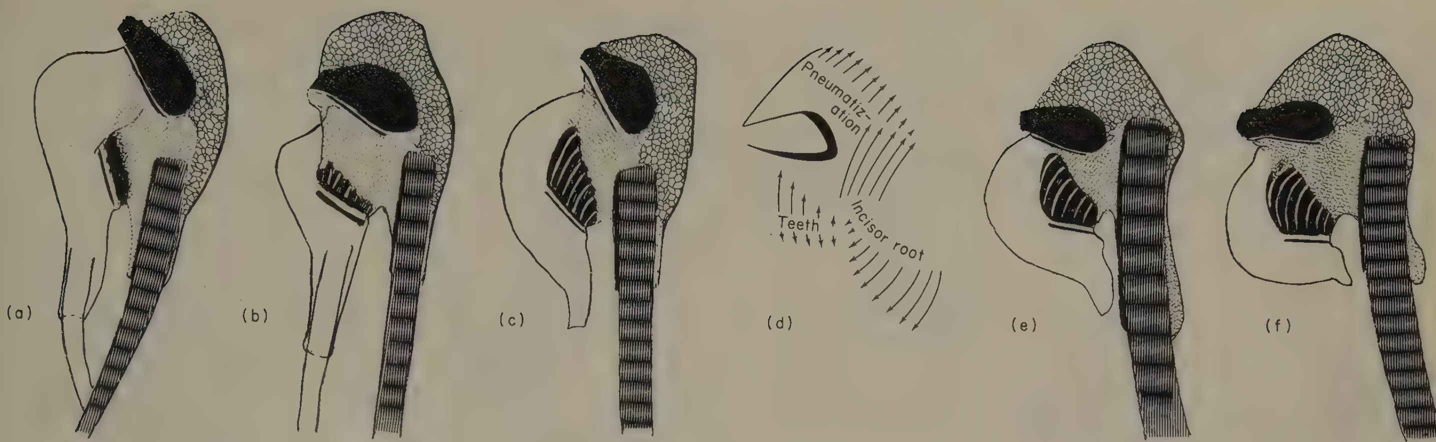
The tusks of some early proboscids may have been adapted for prising food loose or shovelling up vegetation but it is more likely that the principal function of proboscid tusks was related to intraspecific competition. There were great variations in tusk form and mandibular architecture but most of them can be interpreted as devices for combat. Where the tusks could interlock the antagonists could enhance the tie by grappling with their trunks. This combination can be seen in the ritualized contests of modern elephants.

Judging by the shape, the slenderness and the relative lack of reinforcement of the skull, the four-tusked gomphotheres may have fenced with the tips of their long tusks but it would have been a clumsy business and the changes that led to modern elephants may be first apparent in *Stegotetrabelodon* where the roots of the exceptionally long mandibular tusks turned down at an angle to the toothrow and the basi-cranial axis.

In living elephants the functions of tusks are obvious. All forms of intraspecific competition are asserted at the point of a tusk. Amongst adult males this takes the form of fighting for oestrous females, in the younger males tusks come into play during frequent sparring. For females with a family group, access to food or other resources may be determined by a stable hierarchy but the ultimate test of any competition is likely to involve tusks, and mature females, particularly matriarchs, regularly drive off their male offspring when their harassment of other members of the family becomes intolerable. For such tasks the female must be as well armed as the young male.

In the evolution of proboscids development lay in opposite trends at the front and back ends of the jaws. While the cheek teeth retreated backwards or reduced in number, the incisors and their associated bone increased in bulk and extended forwards. Watson (1946) pointed out that the lengthening of the lower (and sometimes the upper) jaws in early proboscids has a resemblance to the increasing proportional length of the legs.

There are obvious selective advantages for heads that are built to enhance the power of leverage of their own tusks and also protect them from those of their opponents. Contestants must be able to absorb the impact of heavy blows as well as deliver them. Great size increases the momentum of butts, charges or stabs and all the larger species of elephants have cranial superstructures which act as shock-absorbers and reinforcing buffers. These superstructures vary from species to species and their form is influenced strongly by the size of the animal and probably by the fighting techniques and by the shape and position of the tusks. They consist of elevated surfaces where the bone has become extensively honey-combed with air sinuses and

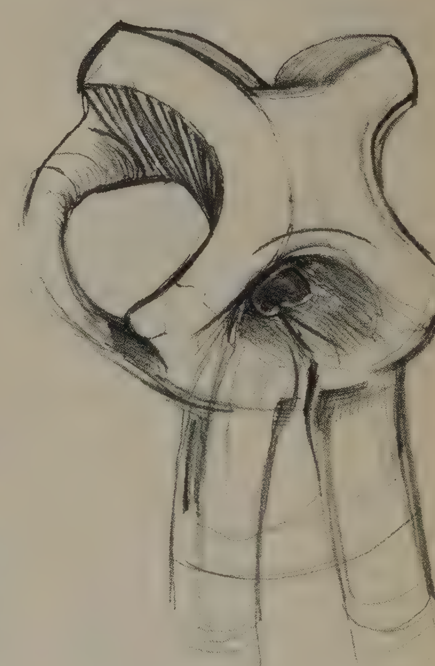


Diagrams to show approximate position of brain and basi-cranial axis in relation to upper incisor root with changes of orientation in more advanced forms indicated in (d). Increase in pneumatization and in the size of the upper tooth row is also indicated. (a) *Gomphotherium* (b) *Stegotetrabelodon* (c) *Elephas planifrons* (d) See above (e) *Loxodonta adaurora* (f) *Loxodonta africana*.

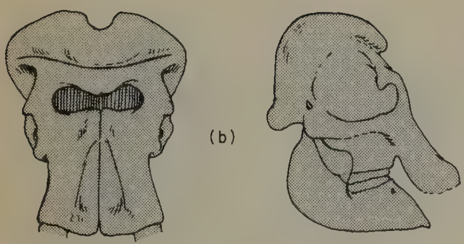
this pneumatic osteotysis around the cranium is responsible for a total remodelling of the elephant skull. The pneumatization follows arcs across the cranium without regard for component bones and sutures, which are obliterated, creating powerful rhythms. These have appealed so strongly to the sculptor Henry Moore that he has embarked on entire series of sculptures and drawings based on the skull of an East African elephant.

The elephant's skull was well described by Gregory (1903), who stressed that it was well adapted to resist stresses and strains and he remarked on built-in resiliency which must also serve to absorb pressures exerted by the leverage of the tusks and by butts or blows.

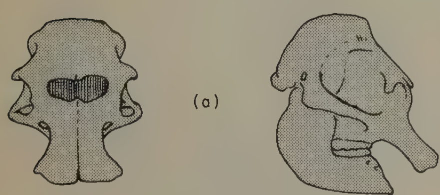
> "The occiput, both in ontogeny and phylogeny, flattens out and rotates backwards, spreading both vertically and laterally, until at last it forms, as it were, a great functionally solid bed-plate, receiving the thrusts of the opposite inverted arches into which the skull has been resolved. Each pair of these symmetrically disposed arches which also connect with the system culminating in the basisphenoid, reacts, of course, against some components of the force transmitted either to or from the tusks, trunk and grinders, or when the forehead is used in pushing. The innumerable toughly constructed air cells of the diploe give immense strength, lightness and especially resiliency. This desideratum may also be the reason for the very loose articulation of the malar with the zygomatic process of the squamosal, which would also permit the facial portion of the skull to bend back slightly under pressure, towards the cranial portion."



These arches are illustrated opposite. They protect the brain from all directions and the orientation of the honey-comb cells also suggests that this structure is designed to absorb all manner of forces. Bridged by the zygoma, the temporal muscles fill the lateral voids of the skull and the neck muscles are attached at the back of an elevated occipital arch or arches. These muscles have been invoked by some authors as the sole determinants of skull form and there is no doubt that muscle leverage is increased and improved by heightening of the skull but there have been elephant species in which there was no elevation of the temporal region and muscle leverage

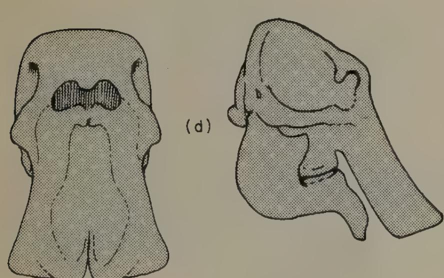


(b)

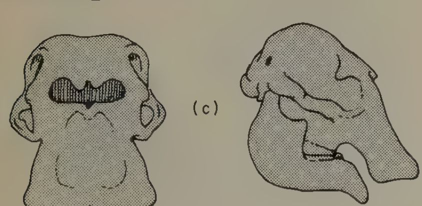


(a)

Is the forest elephant an ancient ecological isolate of the Pliocene *Loxodonta adaurora*? Skulls showing (a) *Elephas falconeri*, a dwarf island form of (b) *Elephas namadicus* (c) *Loxodonta africana cyclotis* and (d) *Loxodonta adaurora*.



(d)



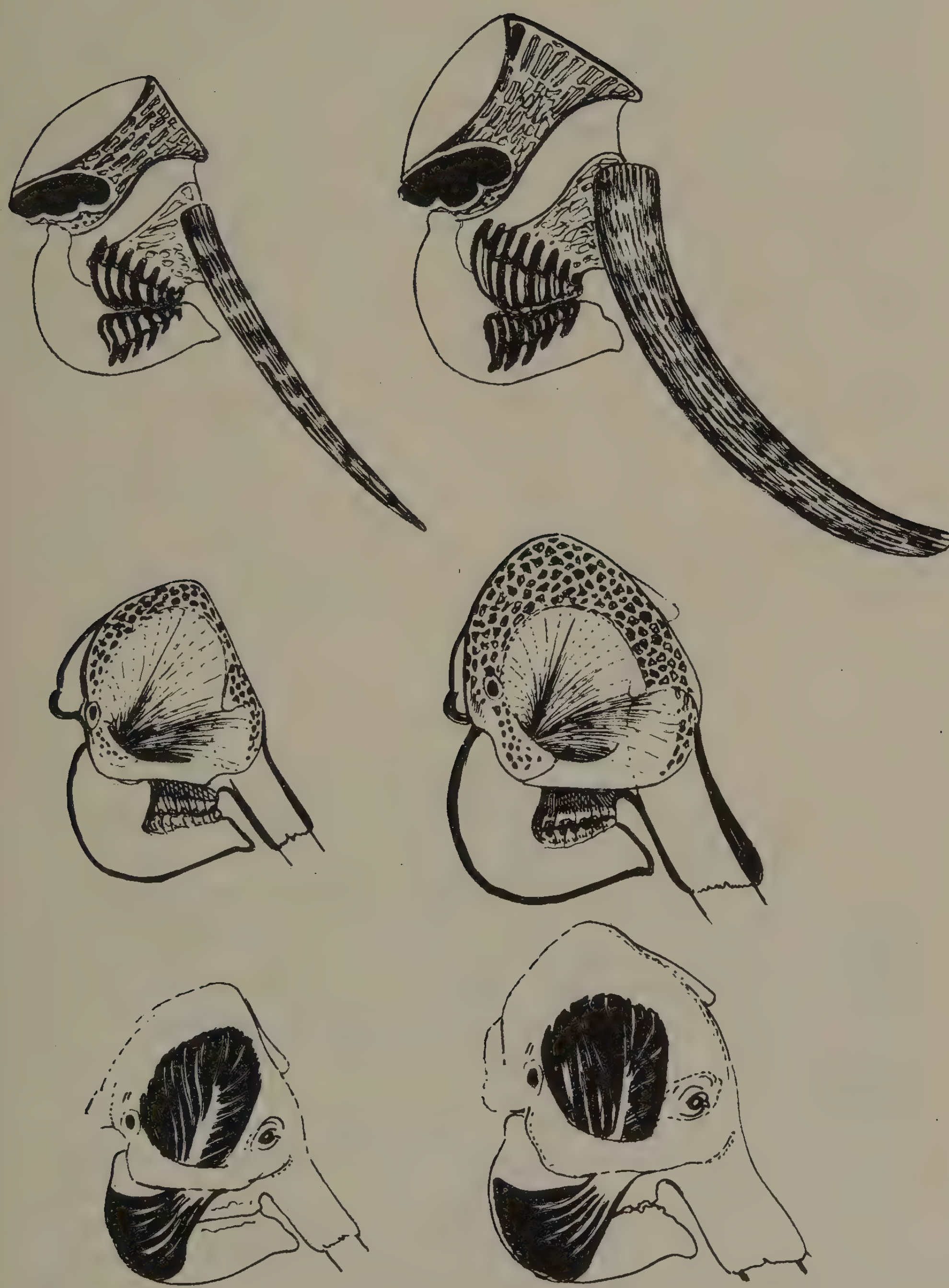
(c)

does not explain pneumatization nor the elaborations of form that distinguished quite closely related species of extinct elephants.

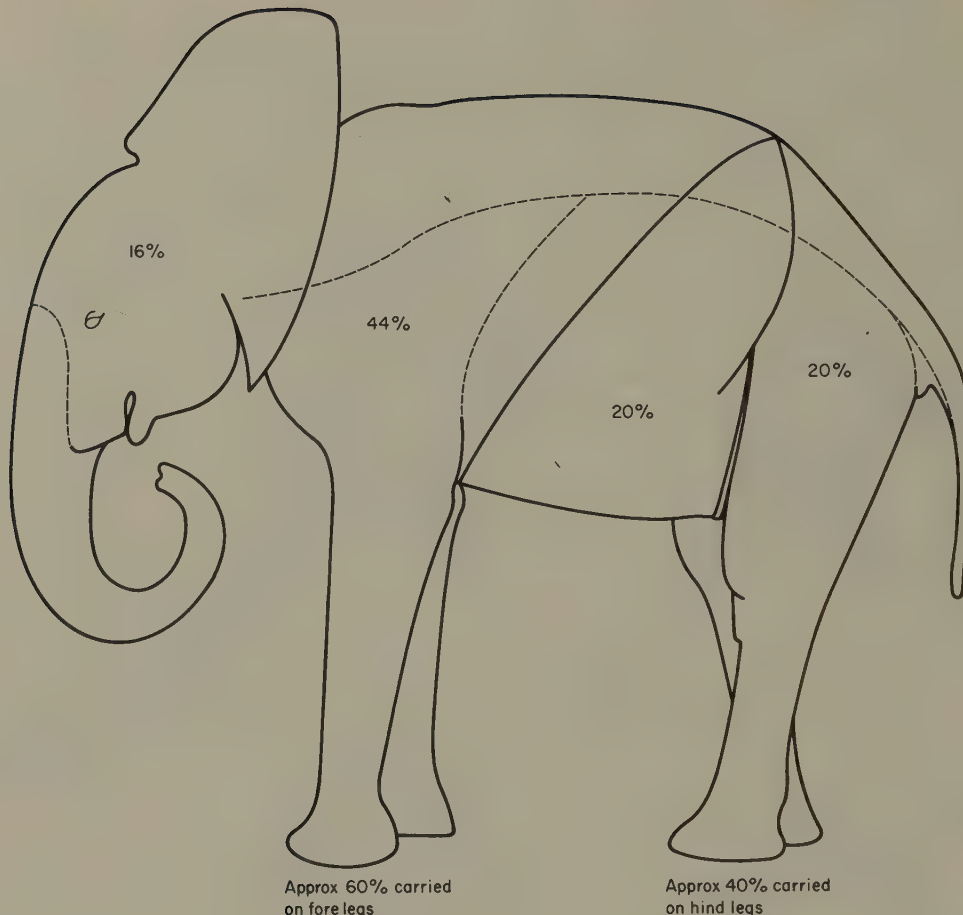
Elevation of the temporal region occurred at different periods in the evolution of African and Asiatic elephants but in both lineages it appears to have been correlated with the roots of the tusks changing their orientation. From being approximately aligned with the basi-cranial axis they rise to a vertical position in which the roots come to lie at the front of the face. Adequate sockets for the large realigned tusks were provided by vertical deepening at the front of the skull, while the simultaneous rise of the occiput at the back improved muscle leverage. Extensive pneumatization of the proboscid skull is associated with this wholesale raising of the table of the head.

Amongst the many varieties of Pleistocene elephants *Elephas namadicus* was widely distributed and common in Eurasia at the end of the Pleistocene. This species was the size of a modern African elephant and had an enormous hood of air-inflated bone which covered over the top and sides of its cranium. Isolated on the Mediterranean islands of Sicily, Cyprus and Malta, this elephant declined in stature and a half-size form, *mnaidriensis*, existed in Sicily for half a million years (Ambrosetti, 1968). During the last glaciation progressive stunting culminated in the dwarf elephant, *E. falconeri*, which Ambrosetti considered to be the product of confinement to a limited habitat during extreme climatic conditions. The differences between *E. falconeri*, *E. mnaidriensis* and *E. namadicus* can be related to size, among the most striking of which is the greater skull pneumatization of the larger species (see illustrations). Paedomorphism is common in small species, but the rounded cranium and gracile proportions of *E. falconeri*, which stood only one metre at the shoulder when adult, show that reinforcement of both limb bones and cranium are linked with size and weight. Furthermore there are similar cranial differences between small- and large-sized forms in other elephant stocks. A broad but shallow plate of pneumatized bone covered the forehead of the moderate sized *E. planifrons*, while the brain of its larger relative *E. hysudricus* was encapsulated by a prominent bonnet of honeycomb bone. The living forest elephant *L. africana cyclotis* also shows very much less pneumatization of the skull than the larger savanna elephants. Such differences in shape and depth cannot be correlated directly with masticatory efficiency nor with the presence or absence of tusks. Cranial buffers are more developed in the males of both living elephant species and even more extreme sexual dimorphism can be inferred for some extinct elephants and mammoths. Degrees of pneumatization are therefore likely to have had some correspondence with the size and sex of elephants while the external shapes of specific crania were probably influenced by the angles of temporal and neucal muscles (see pp. 22, 38), by the orientation of basi-cranial axes and by specific fighting styles.

While many authors have suggested that air sinuses are an adaptation to lighten the elephant's skull (Badoux, 1961), Young (1950) suggested, instead, that the tusks might serve to make it heavier to act as a counterweight for the purpose of balance. I pointed out in Volume I that heavy weights of ivory alter the dynamics of stance and gait. However, it should be remembered that the trunk weighs as much as the tusks in all but the largest tuskers and balance must be strictly subsidiary to the more fundamental role



Three aspects of skull structure in female and male *Loxodonta*. Above: Cross-section showing brain capsule, honeycomb bone and rooting of molar and incisor; Middle: Extent of cranial buffering; outer surface "shaved" to reveal honeycomb; Below: Position of *masseter* and *temporalis* muscles.



Weight distribution in African elephant. (Data from (tuskless) I. Parker.)
Trunk 5%;
Ears 1·2% × 2;
Rest of head 9·1%;
Atlas to pelvis and ribs 12%;
Heart and lungs 1·5%;
Viscera (beyond diaphragm) 35%;
Pelvis and tail 6%;
Forelegs 7·5% × 2;
Hindlegs 7% × 2;
(tusks can weigh up to 6%, very rarely 8%, of total bodyweight).

of the tusks. The actual distribution of weight in an African elephant is shown in the diagram above (data from I. Parker). Because heavy weights cannot be carried on a bent limb elephants have columnar legs. Toes are contained at the base of the column within a hoop of tissue, skin and nail. Beneath the toes there is a cushion of elastic tissue which bulges the sole of the foot when the weight is off and flattens out to form a flexible pad at every step. The limb function and gait of elephants has been compared with that of the rhino and dinosaurs by Bakker (1971) and he has categorized the elephant as a large ambler.

The proportions of elephants enhance stability through the shortening of the lower limbs and extension of the humerus and femur. The ilium is greatly expanded.

Another very important development in the Proboscidea was the enlargement of the brain. This is only partly due to an overall proportional enlargement and there is no doubt that elephants are exceptionally well co-ordinated and intelligent. An extended period of growth and learning within a stable family group allows the young to benefit from the experiences of the old. For the long-lived elephants the existence of "traditions" might have become an important factor for their survival and success.

Foot of elephant to show pad.

The proboscids are known to have originated in Africa but in the absence of early Eocene fossil deposits an ancestral form has to be envisaged by reference to an animal which was probably more closely related to the sirenians (see Vol. I, pp. 55, 388). This species, *Moeritherium*, is known from relatively complete material from the upper Eocene beds at Fayum. *Moeritherium* may have been wholly aquatic and several features of the skull exhibit sirenian rather than proboscid traits. Andrews (1906) pointed out its sirenian affinities and noted in particular its weak pelvis and long heavy tail. The very short legs of this animal have led some students to envisage the ancestral elephant as exceptionally short-legged, a guess that might very well be mistaken. While the sea of Tethys lay between Africa and Eurasia subungulates and anthracotheres were the dominant African herbivores. The proboscids, hyracoids and sirenians derived from a common subungulate ancestor and their radiation might have begun with adaptation along an ecological gradient. At one end the hyracoids remained wholly terrestrial, at the other the sirenians became progressively more aquatic. Proboscids probably emerged from a stock that had adapted to niches in between these extremes. Even today the existence of various species of water buffaloes, pigs and pigmy

1(a) Hypothetical ancestral proboscid.
1(b) Oligocene tapir *Protapir validus*.
2. Integrade.
3. *Phiomia minor*.
4. *Gomphotherium angustidens*.
5. *Stegotetrabelodon syrticus*.


1(a)


1(b)


2


3


4


5

hippo in areas of tropical swamp forest demonstrates that there are opportunities for large semi-amphibious herbivores. However with the insight provided by knowledge of convergent evolution it is likely that the most exact living equivalents for the first proboscids are the tapirs.

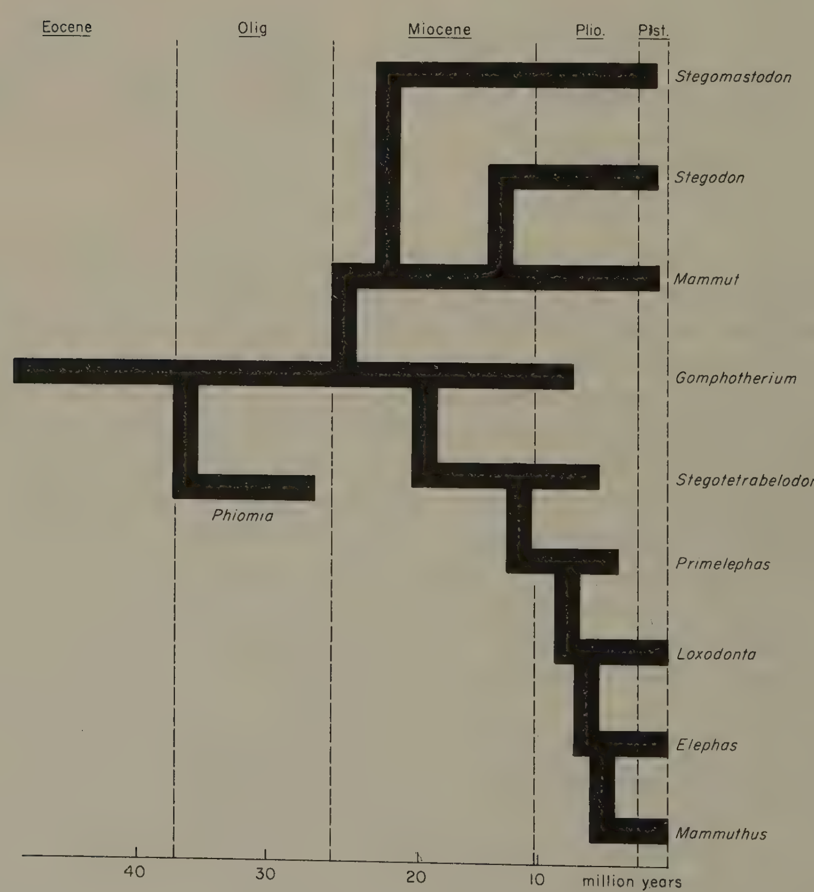
Just how closely convergent early proboscids and tapirs might have been has emerged from an exercise designed to demonstrate that *Moeritherium* had evolved beyond the point where it could reasonably be regarded as a proboscid ancestor. A *Moeritherium* skull is illustrated in Volume I, p. 388 beside those of extinct dugongs and its sirenian affinities are obvious.

On the assumption that proboscids emerged from a less specialized subungulate I used co-ordinate grids to compare skull profile views of an early proboscid, *Phiomia*, with hyracoids and more generalized primitive mammals. I then plotted two hypothetical intermediate forms. These resemble *Moeritherium* in some features but their overall proportions are strikingly similar to those of tapirs. *Phiomia* is unquestionably a proboscid and by the Oligocene the order had begun to diversify. Elephant bones are conspicuous, their teeth preserve well and an abundance of proboscid fossils from all over Africa, Eurasia and the Americas have provided evidence of a fascinating evolutionary spectacle in which elephants eventually became the dominant giant herbivores, many of which only become extinct in late Pleistocene or recent times.

If the earliest proboscids were swamp dwellers their habitat would have offered abundant food even for very large animals but their range would have been severely circumscribed.

Seasonal changes might have encouraged annual cycles of movement in and out of swamps but climatic changes in the Miocene and Pliocene are almost certain to have forced some populations into a wider range of (drier) habitats. In competing with more specialized herbivores bulk feeding may have had some advantages while large size probably offered a certain immunity from predators.

Swamps offer great quantities of relatively soft vegetation and bulk feeders in such a habitat are unlikely to have been discriminating. However an unselective diet in drier habitats probably required a larger range and put greater demands upon the teeth. Some of the early proboscids were large animals but their molars were unsuited to a tough diet and it is significant that of the later proboscids the two pre-eminent families, elephants and stegodons, both altered the structure of their teeth in an obvious accommodation to more difficult diets.



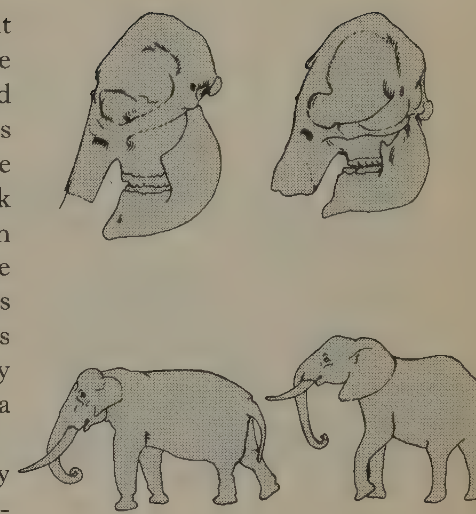
Tentative schema of proboscid radiation.

Various reconstructions of proboscid phylogeny have been attempted but widespread convergence or parallel evolution within the Order and the existence of considerable individual variation contributed to a confused picture until very recently. The major difficulty arose over the Mastodonts which were already a distinct group in the Oligocene and subsequently gave rise to the Stegodonts. The latter included forms with the stature, tusk development and general appearance of modern elephants. Yet their teeth differed in being heavily cusped and relatively short-crowned. So close were the resemblances between elephants and stegodons that the two lineages have been mistakenly allied by taxonomists for 130 years. The true affinities of the Elephantidae, which are discussed in the next profile, have only emerged in the present decade as a result of new fossil finds in eastern Africa (Maglio, 1970a, 1973a).

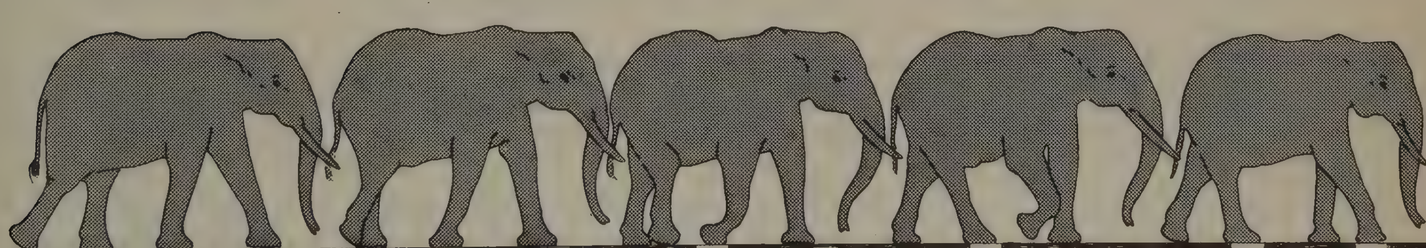
In the course of their evolution the diversity of proboscid forms is truly extraordinary. Fossils from many periods and regions show weird conformations and very varied proportions and sizes. Branching into at least four major lines by the end of the Oligocene the proboscids had radiated into some fifteen phyletic lines by the end of the Miocene and this proliferation accelerated in the Pliocene.

Yet it is perhaps even more extraordinary that some of the most persistent Pleistocene survivors of this Pliocene radiation, including the living elephants, should have been so closely alike in form, in spite of the remoteness of their common ancestry and the dissimilarity of their more immediate relatives.

When we consider the great array of extinct relatives the existence of convergent forms must enhance the value of the surviving elephants as truly representative samples of the most consistently large-sized land mammal Order ever to have evolved.



Convergence in proboscids.
The Asiatic *Stegodon ganesa* (skull from Falconer and Cautley, 1847), (reconstruction from Osborn, 1942) compared with contemporary African elephant.



Pacing elephant. Note placing of hind foot on spot vacated by forefoot.

Elephantids

Elephantidae

Recent years have seen unprecedented discoveries of fossil hominids from many new Pliocene and Pleistocene sites (see Volume I, pp. 102—5). Most beds have yielded abundant proboscid remains revealing that the true elephants or Elephantidae evolved in Africa with startling rapidity and, like the hominids, seem to owe their success to an adaptive shift out of rich moist environments into more open and difficult habitats.

Elephants are diagnosed by their teeth, partly because this has been normal taxonomic practice and in a largely extinct Order the teeth are the most frequently preserved (and most portable) remains and partly because it really is the molar teeth that distinguish true elephants from other superficially very similar proboscids. The rich array of fossil teeth also provide clues to the evolution of elephants.

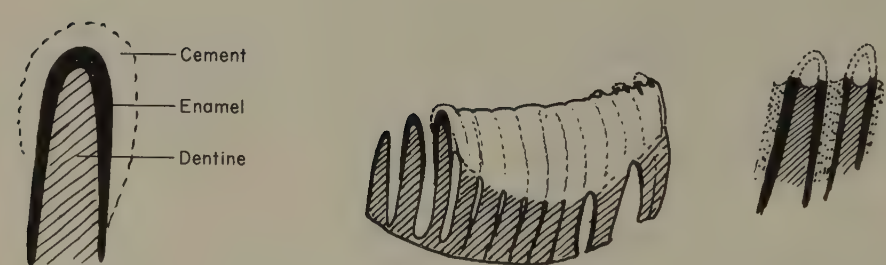


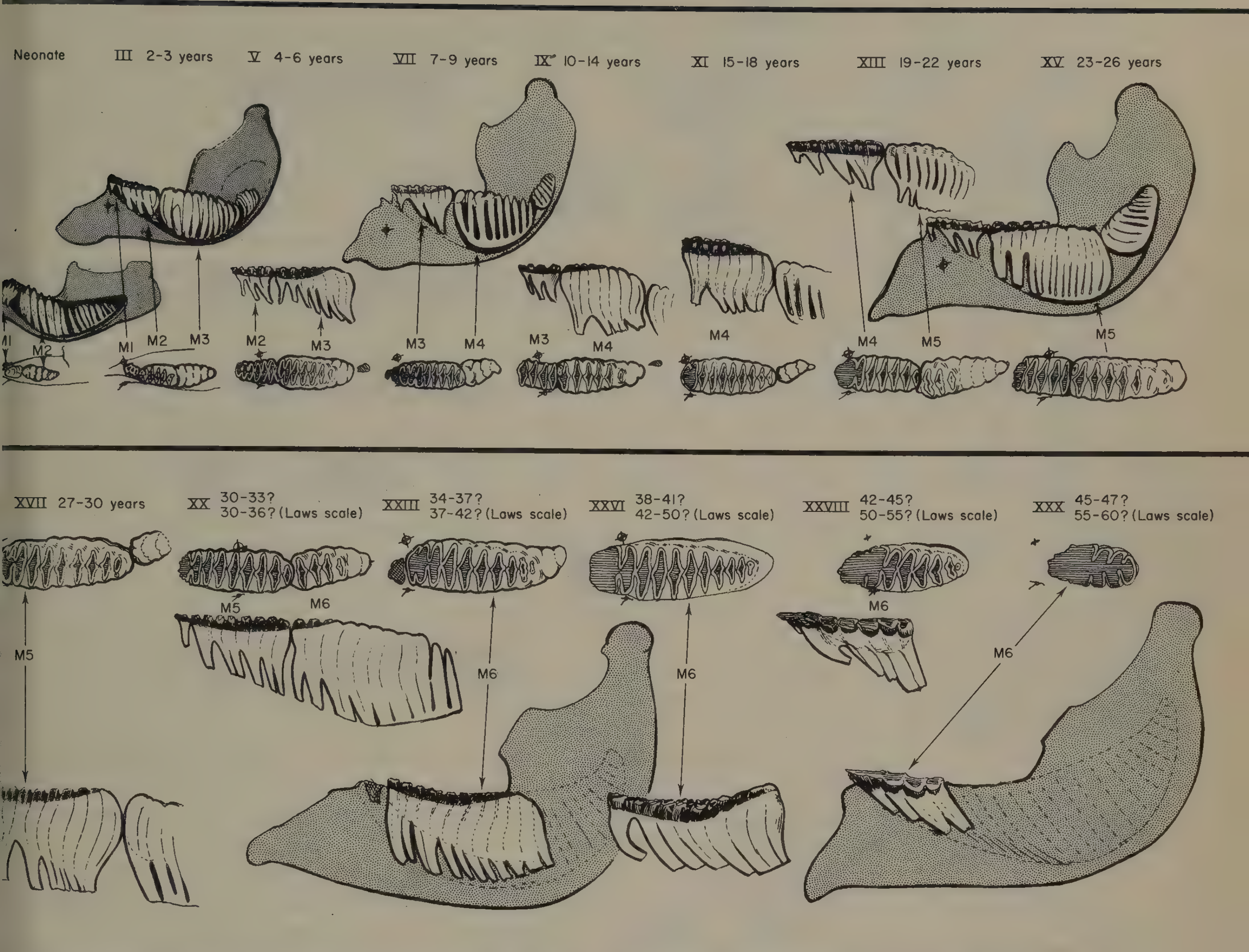
Diagram to show development and wear of elephant molar.

The molars are composed of a series of conical dentine plates covered in enamel and invested in a cement matrix. No more than one and a half teeth are in use at any one time and during its functional life each tooth effectively fills the short jaw.

In the course of an elephant's life six cheek teeth succeed one another.

The three milk molars resemble the adult dentition and erupt like them in a one by one sequence.

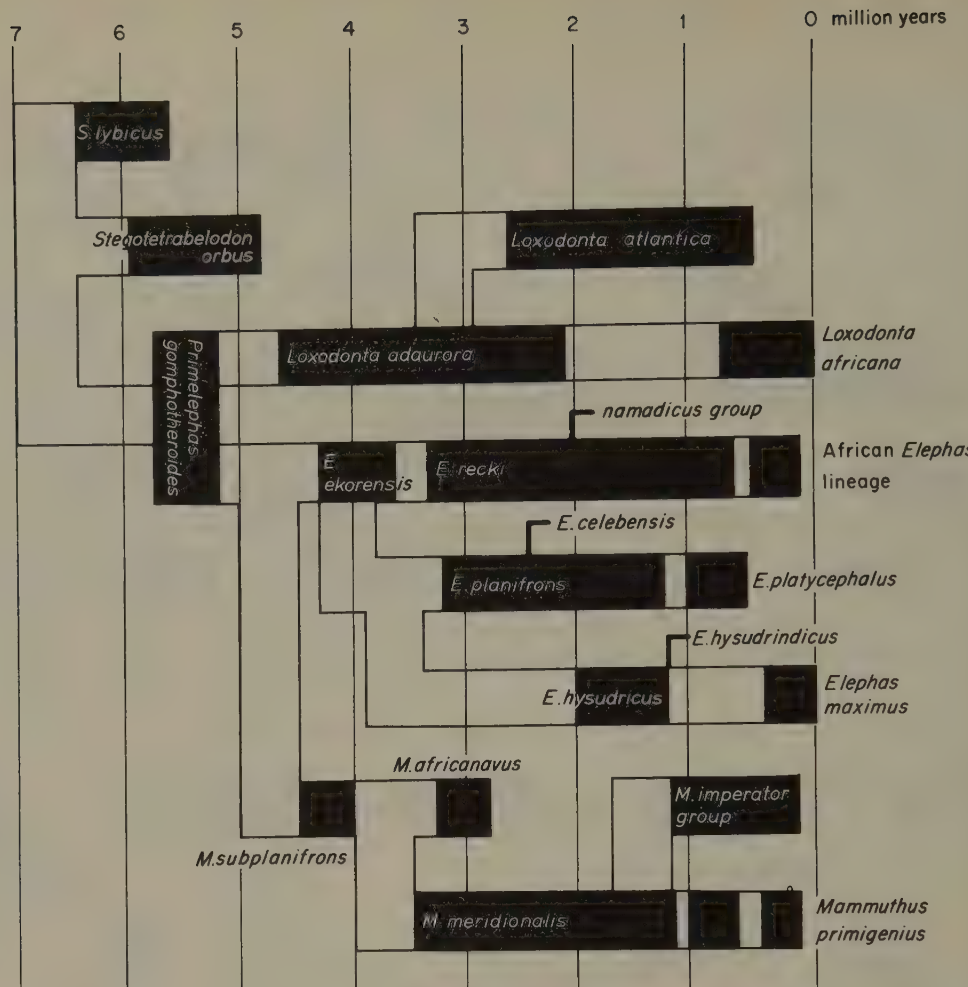
The teeth are tilted and travel along the jaw at an angle which is steeper in the upper jaw than in the mandible. The forward surface of the molar is worn down progressively while the roots are also resorbed towards the front so that the remnant drops out without difficulty once its effective grinding surface has been used up. When the entire sequence of molars has run its course the elephant can no longer masticate its food properly and malnutrition sets in to hasten death. An elephant is therefore as old as its teeth and age can be estimated for elephants on the basis of the molar sequence and tooth wear (see diagram and Laws, 1966).



Toothwear and progression in the African elephant. Roman numerals indicate age groupings according to Laws (1966). Age assignments are tentative particularly after 30. M1 to M3 are equivalent to milk molars in other animals. As all teeth are deciduous in the elephant molariform teeth are numbered 1—6.

In the phylogeny of elephants the dominant progressive trait was the deepening of the tooth and the multiplication of molar plates and this culminated in the modern Asiatic elephant, *Elephas maximus*, and the recently extinct *Mammuthus primigenius*.

Recent finds from the new Pliocene and Pleistocene fossil sites in eastern Africa has shown that the family emerged in Africa from the four-tusked *Stegotetrabelodon* (Aguirre, 1969a; Maglio, 1970a, 1973b) and that after an initial radiation within Africa ancestral *Mammuthus* and *Elephas* entered Eurasia and evolved forms that are among the most extreme in the family.



Dendogram of elephantid radiation (after Maglio, 1973a).
Black = known time span.

Within Africa, *Elephas* was also the dominant line throughout the Pleistocene and progressive changes in the teeth of the *E. recki* lineage have proved to be an important aid in stratigraphic correlations (Maglio, 1970a, 1972a, 1973b; Cooke and Maglio, 1972).

Among long-lived animals needing to eat great quantities of coarse roughage it is clear that there was an adaptive advantage in improving the efficiency and prolonging the life of the teeth and the origins of this elephantid trait can be traced in the families' immediate ancestors, the gomphotheres, which are represented in East Africa by *Gomphotherium* species from the lower Miocene at Rusinga and upper Miocene at Ngorora.

The enamel was very thick in the molars of these proboscids but the teeth were also elongated from front to back, which required a reorganization of tooth succession to accommodate them in a relatively short jaw. The three milk molars provided the first chewing surface after erupting in succession. These were displaced by the third and fourth premolars which were in turn replaced by a succession of slightly tilted molars so long that only two could be accommodated in the jaw at a time and old gomphotheres, like elephants, ended up with a single tooth which, like its predecessors, wore away from the front. Cusps occluded into basins and mastication was achieved by a forward grinding action that eventually wore the points off the cusps and exposed sharp enamel ridges that were aligned across the tooth.

As an individual gomphothere aged the wearing away of the cusps altered the way it chewed. When the crowns no longer interlocked the jaws

were free to travel back and forth and effectively shred the food so that a grinding-mill action was replaced by a forward grating action. Thus the phylogenetic development of elephantine dentition and its function was partially anticipated in gomphothere ontogeny.

The connexion between gomphotheres and elephants was first identified by Aguirre (1969b) in a brief review of the Elephantidae. Examining a little-known Pliocene proboscid, *Stegotetrabelodon*, (which had been described by Petrocchi in 1941 during the Second World War) he pointed to the combination of gomphothere and elephant-like structures in the enamel ridges of the molar teeth. With excavation of new Pliocene beds in Kenya this genus proved to have been a dominant proboscid between seven and four million years ago. Its remains co-exist with those of a variety of newly discovered primitive elephants found in the Baringo–Turkana area by the East African Geological Research Unit and an expedition from the Museum of Comparative Zoology, Cambridge (Mass).

A member of the latter expedition has described all the proboscids discovered in East Africa over the last decade and has published an important revision of the Elephantidae (Maglio, 1973b).

Maglio classified *Stegotetrabelodon* as an elephantid and the three known species illustrate the transition from four-tusked, low-crowned gomphotheres to two-tusked, high-crowned elephants.

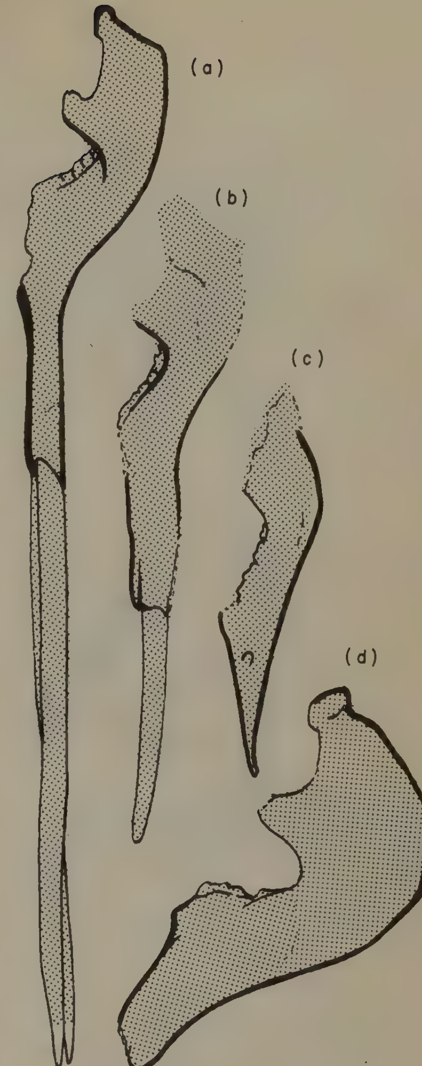
The most primitive species, *S. lybicus (syrticus)* has a shallow down turned mandible with very long thin tusks. The molar crowns are less compressed than in *S. orbus*, which has thinner enamel, deeper valleys between the molar plates and shorter lower incisors. The third species has been named *Stegodibeledon* (Coppens, 1972) because it was without mandibular tusks; like most elephants.

Small mandibular tusks are known to have been retained (or perhaps reappeared) in at least two elephant species, the pigmy *Elephas celebensis* and *Primelephas gomphotheroides*, so named in recognition of its primitive status.

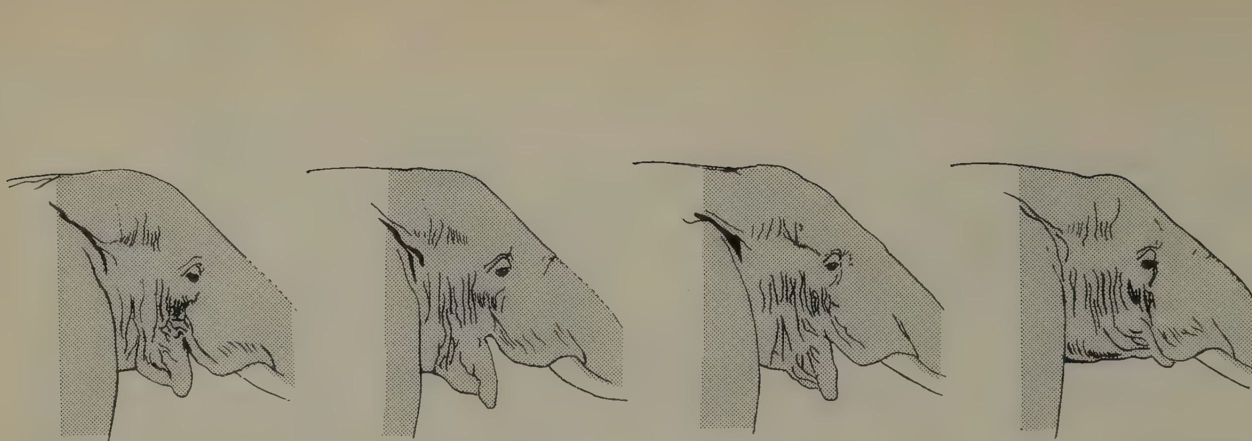
Maglio (1973b) has postulated that all the elephants belonging to three major lineages derive from *Primelephas* stock (see dendrogram and diagram). Only the teeth and mandible of this and several other elephant species are known but there now exists such a wide array of fossil elephant molars from representative levels of the African and Eurasian Pliocene and Pleistocene that a clear picture of the families' dental evolution can be traced and its significance has been summarized by Maglio (1973b).

> "The dentition of the earliest elephants did not differ basically from that of the gomphotheres but a number of important changes occurred which seem to reflect a functional shift in mastication. As the elephant tooth became longer and was unaccompanied by any lengthening of the mandibular corpus there was less room in the mandible. This resulted in fewer teeth in the jaw at any given time. The greater complexity of the milk molars functionally extended the tooth row forward and made efficient molars of the adult type available at an earlier age. . . . The major adaptive change that characterised the rise of the Elephantidae seems to have been a rapid reduction of the grinding components of mastication in favour of the shearing component."

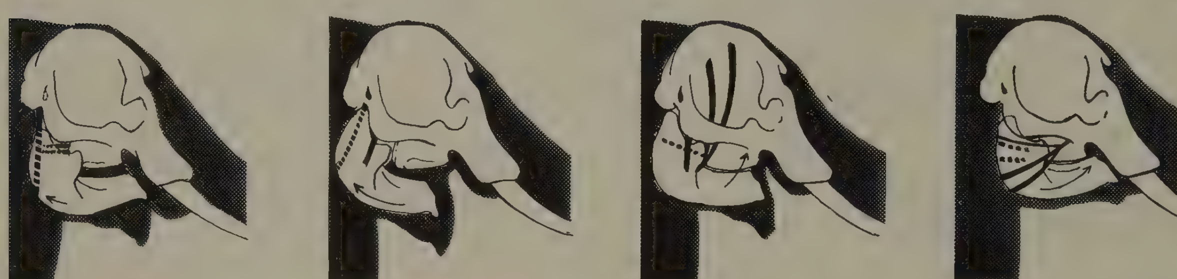
Earlier, the skull of the African elephant was compared with those of its fossil ancestors. In the following profile I shall examine the mature male



Above: Lower jaws of:
(a) *Stegotetrabelodon lybicus*;
(b) *Stegotetrabelodon orbus*;
(c) *Stegotetrabelodon schneideri*;
(d) *Loxondonta adaurora*
Below: *Primelephas gomphotheroides*: reconstruction.

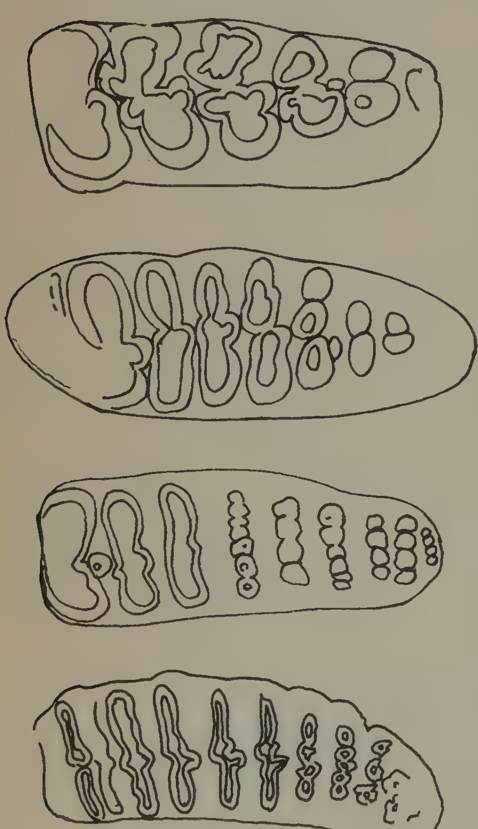


1 2 3 4



Primelephas gomphotheroides: reconstruction.

Below: (from top to bottom)
Gomphotherium;
Stegotetrabelodon;
Primelephas gomphotheroides;
Loxodonata africana.



skull as a structure adapted to fighting. At this juncture the skull can be considered in the context of that elephantid speciality, rasp-chewing by deep single teeth set in short jaws. Elephant mastication has been analysed in detail by Chang (1929) and Maglio (1972b, 1973b) and the mechanism will only be summarized here.

The short heavy mandible hangs from the *temporalis* muscle like the chair of a swing. This is because the *temporalis* is effectively at right angles to the jaw and because the coronoid process is so far forward that its centre of gravity lies immediately below the *temporalis* insertion. Forward movement is achieved through contraction of the *masseter*. This allows the jaw to swing backwards and forwards along an arc which corresponds with the occlusal surface so that the molar faces form curved ellipses. The entire jaw can travel back and forth because the condyle also slides to and fro over the curved squamosal. Observation of a chewing elephant (see frames from film :drawing above) allows one to appreciate the surprising throw of the jaw in spite of the confined space within which it moves.

Describing the human jaw mechanism, which is also short and sharply angled, Gingrich (1971) pointed out that the mandible acts as a link between the forces exerted by the muscles rather than as a lever. This is even more true for elephant mastication where the action requires a longer and more forceful swing of the jaw.

The jaw ceases to be a lever when the condyle leaves the post-glenoid depression. At this moment contraction of the well developed lateral *pterygoid* muscle provides an elastic pivot. The teeth part, close over the food and mastication by shearing action is achieved by the teeth grating forward under pressure. When this forward swing is spent the teeth part and the *digastric* pulls the jaw back and up again into the post-glenoid depression.

Evolution of the elephant molar is shown (margin, below) in drawings of the surface and section of M_3. These illustrate the tilting of the tooth, its increasing depth and number of plates and progressive thinning of the enamel ridges.

These developments took place separately in both Asiatic and African branches of *Elephas* and culminate in their most extreme form in the mammoth.

Deepening a tooth prolongs its life, while increasing the number of plates and thinning the enamel are both devices to enlarge the abrasive surfaces of the molar but it is clear that if the enamel becomes too thin efficiency is reduced, wear speeds up and the working life of a tooth is shorter. Effective mastication must also demand minimum distances between ridges below which the shearing action is impaired. Among other things the absolute size of the elephant and its tooth and the texture of its food must influence the thickness and distances at which the ridges can perform their role effectively.

The influence of body size on tooth structure is clear in the teeth of dwarf isolates which do not shrink their teeth proportionately but instead have relatively fewer plates and broader spaces than their large mainland relatives.

Reduction in body size and hence in consumption may have been one option that was open to elephants wherever bulk diets were difficult to sustain as is likely to be the case on small islands and other habitats with limited resources.

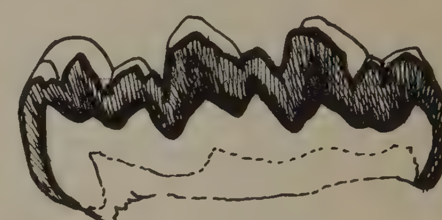
High-crowned, multi-plated teeth of *Elephas* type may have been of less functional value for small-sized elephants and may have been less useful for certain food types. This will be discussed further shortly and may have a bearing on our understanding of the past and present status of the African elephant.

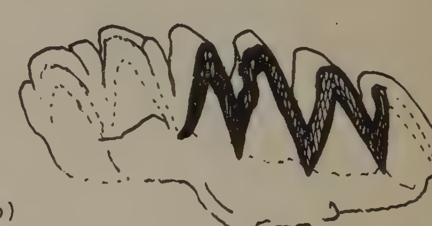
In the number of plates and in conformation the teeth of *Loxodonta* resemble those of *Elephas* dwarfs that formerly lived on Sicily and Malta. However, fewer and more widely spaced plates are also primitive features, as is the relatively low crown and this is undoubtedly the case for *L. africana*.

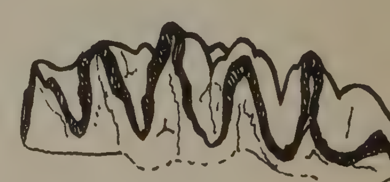
We have good fossil evidence of primitive status for the *Loxodonta* genus in *L. adaurora*, which is a common elephant in African Pliocene deposits. This elephant had lost its lower tusks but retained cavities in its hooked mandible. The upper tusks of this species were enormous. Such a gross enlargement of the upper incisors coinciding with loss of the lower ones would have introduced mechanical problems of anchorage for the tusks. In the case of *L. adaurora* it is clear that the solution to this was cranial flexure so that the tusks became embedded vertically down the face rather than horizontally along the basi-cranial axis, as in *Elephas planifrons* and *Mammuthus meridionalis*, its contemporaries in Eurasia. To compensate for the loss of a deep cranial root for the tusks, *L. adaurora* developed massive bony sheaths.

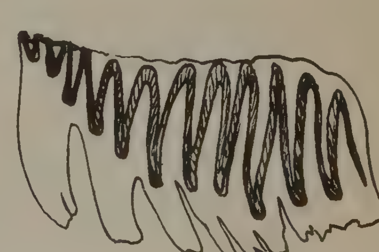
Sharp down-turning of the face made for a prominent forehead and brought the temporal fossa forward. This has the probably incidental but subsequently very significant effect of making the *temporalis* vertical to the tooth row so that this elephant was the first to achieve a balanced jaw mechanism of the type just described. It also elevated the temporal region as can be seen in a comparison with *E. planifrons*.

Evolution of elephant teeth. Enamel layer (hatched) overlying dentine cones and invested in cement.
(a) *Gomphotherium angustidens*;
(b) *Stegotetrabelodon orbus*;
(c) *Primelephas gomphotheroides*;
(d) *Loxodonta africana*.


(a)


(b)

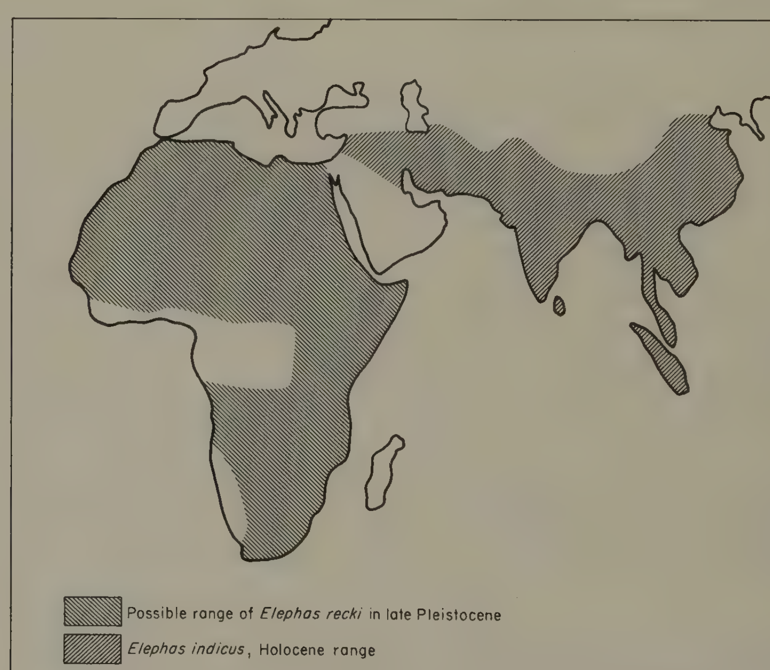

(c)


(d)

This early improvement in musculature economy and muscular balance might have partially offset the disadvantage of shallow crowns. It was only much later that *Elephas* and *Mammuthus* also developed facial flexure and Maglio (1972a) has observed:

> "It has usually been assumed that the African elephant was persistently conservative in its dentition, which is clearly least evolved from the ancestral condition. But other evidence reveals a remarkable convergence in cranial structure of both *Elephas* and *Mammuthus* toward the plan already achieved by *Loxodonta* more than 2·5 million years earlier.
>
> During the first two-thirds of their history, both *Elephas* and *Mammuthus* retained a more or less gomphothere-like cranial organization except for some structural changes related to fore and aft shearing. . . . This combination of relatively specialized shearing teeth and a less specialized skull and muscle configuration in the earlier stages of both genera seems to have been sufficient adaptation for the particular ecological requirements of these forms (probably woodland to open savannah in both cases). In *Loxodonta* on the other hand, the cranial architecture and associated musculature seem to have specialized early. Little change in the dentition occurred during the entire history of the genus and it would seem that this particular combination of cranial and dental specialisations was sufficient for this group. It is interesting to note that *Loxodonta* never expanded its range beyond Africa, where environmental conditions seem to have been relatively stable as compared with Eurasia."

After two-and-a-half million years in which it remained virtually unchanged, *L. adaurora* disappeared from the fossil record by which time it had been replaced by the more advanced *Elephas recki* lineage, fossils of which dominate all deposits throughout the entire Pleistocene period.



So where was the African elephant during the Pleistocene and can we account for the changes that have occurred in skull morphology between *L. adaurora* and *L. africana*?

During the extended period of loxodont dominance these elephants probably lived in all habitats (as they do today) and this must have included true forest, a habitat which has scarcely changed since the Miocene, where browse is scattered and not very abundant and herbaceous growth only occurs in glades and river courses where the canopy is broken. Within this moist, closed environment there would have been less selection for ever more efficient teeth than for social adaptation and for accommodation to a sparsely distributed food supply. In such circumstances somewhat smaller body size may have been an advantage. Effective use of the habitat would probably favour an ability to disperse in minimal social units. Above all, the means of maintaining contact within these groups would need to be exceptionally well developed in a dense habitat.

Elephants in forest do not normally suffer from extreme annual fluctuations in climate and in the quantity and quality of their food, they can therefore live a stable existence. We know that the contemporary forest elephant does not change its habits very greatly around the year. Stable groups follow regular circuits, their movements being contained within the boundaries of well-known home ranges (Offerman, 1953).

Forest elephants are consistently smaller than savanna elephants but they also grow and mature more slowly and it is possible that some of the physical differences between them are partly due to qualitative differences in diet and to the effects of exposure to sun. Maturation rates influence skull form, particularly in male elephants and it is certain that the original descriptions of various forest dwelling dwarfs took little or no account of these factors. Nonetheless, there has been a general consensus to recognize the distinctness of the two populations with a division of the species into a forest dwelling race, *Loxodonta africana cyclotis* and the bush elephant, *L. africana africana*. This division is paralleled by the buffalo (see Volume IIIC).

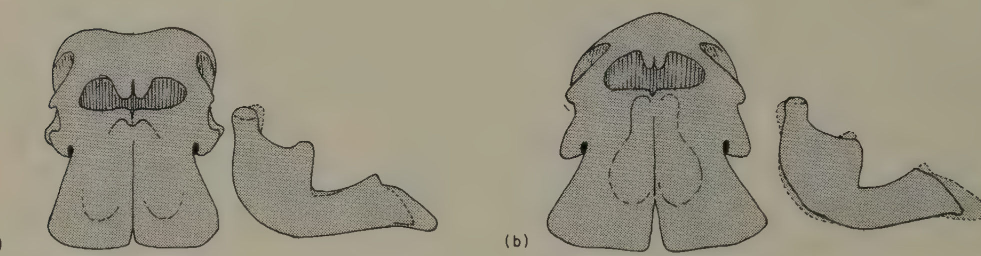
Did forests continue to harbour *Loxodonta* long after *Elephas* had become the dominant Pleistocene elephant? If nothing else, the fossil record demonstrates that the African elephant fills a broader niche today than the genus did in the Pleistocene. Such palaeontological implications were unknown when Allen (1936) first suggested that the forest elephant might approximate to the original stock from which the larger bush elephant derived. He clearly had in mind the anomaly of its low-crowned teeth; teeth that appear adequate enough for the modern elephant but must have been decidedly inferior in a world of numerous competing proboscids. We now know that even within Africa the crown became higher and higher in the *Elephas* lineage, and culminated in *E. iolensis*, a species that was still present in eastern Africa 40,000 years ago and remains of which have been found associated with a well developed Acheulian industry (Coppens and Gaudant, 1967).

It is clear that such species must have formerly kept *Loxodonta* out of the drier habitats and that they were better adapted to cope with more demanding diets.

Because *L. africana* is relatively unspecialized it is unlikely that its immediate ancestors had found some peculiar and unpredictable niche. It is more generalized and more advanced than the Pliocene *L. adaurora*. The very different proportions of *L. atlantica* of the middle Pleistocene were related to

gigantism (it exceeded even the largest of living elephants in size) and is not eligible as an ancestor.

I have mentioned dental similarities between *Loxodonta africana* and *Elephas falconeri*; there are also cranial similarities, most marked in a comparison with *L. a. cyclotis*, which conform with the general tendency for dwarfs to be paedomorphic. If *L. adaurora* was the precursor of *L. africana*, the intrusion of a somewhat paedomorphic phase into the latter's ancestry would go some of the way to explain differences in their facial architecture. A phylogenetic diminution in overall size would alter the allometry of the skull



Skulls of *Loxodonta africana africana* (right) and *L. a. cyclotis* (left) in frontal view with outlines of mandibles superimposed.

(particularly if the relative size of the tusks diminished) and this would be consistent with the more rounded contours of *L. africana* and the stabilized position of the external nasal choanae. If Allen's proposition is correct, then resemblances between *L. a. cyclotis* and *E. falconeri* might assume significance and illustrate how an elephant with a very conservative type of dentition might have survived without becoming a dead-end specialist. It must also be remembered that the dominance of *Elephas* cannot have left a very wide range of adaptive niches open to other elephants and that specialized niches generally leave their mark in peculiar specialist characteristics.

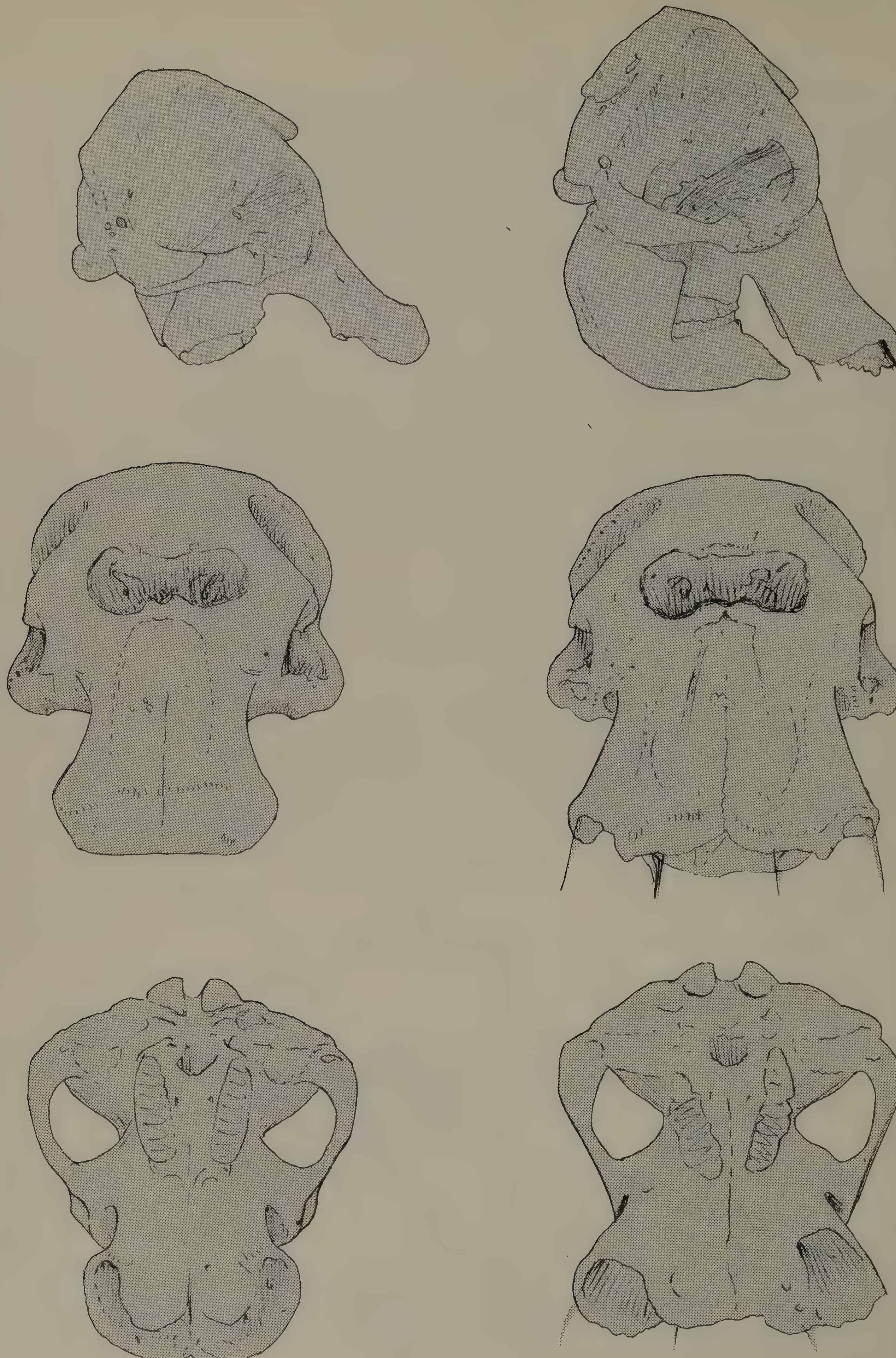
Tropical forest areas in Africa and Asia

Within continental Africa, the role of lowland forests as ecological islands, reinforcing isolation in divergent species and providing a stable refuge for conservative but well adapted fauna and flora has been well documented (see Volume I, p. 28). Invaders do not easily supplant established forest species because the latter are already adapted to conditions that make very different demands, especially on a large-sized herbivore. The conservative status of *Loxodonta vis-à-vis* other elephants favours the idea that this elephant stock made an early adaptation to forest but the most telling argument is our knowledge that *L. a. cyclotis* is a true forest mammal often restricted exclusively to this difficult habitat.

The Ruwenzori elephant that was dissected for this profile is of a type, that appears to be intermediate in character between *L. a. cyclotis* and *L. a. africana* (similar intermediate types occur in Nigeria and elsewhere). However, in forest-savanna mosaics to the north and west and to the south of this area observers have recorded both elephant types co-existing without any apparent gradation of characters, while family groups or herds of the two types remain distinct and do not seem to mix or mingle (Christie, 1924; Schouteden, 1947; Baker, 1953; Kielland, 1971, pers. comm.). Local hunters state that the forest elephants are aggressive and exceptionally vocal and restless. The reputation of forest elephants for aggressiveness can undoubtedly be traced to attempts to approach them in thick cover. Other social animals in the forest also tend to be more noisy (see Volume I, pp. 168, 242; Volume II, pp. 17, 121) and this observation is consistent with the special demands of this habitat.

If *Loxodonta* was restricted to dense habitats for most of the Pleistocene, the species can be expected to retain some of the adaptive traits acquired during this phase of its evolution. Furthermore, such traits might have given *Loxodonta* selective advantages over *Elephas* at some critical point near the end of the Pleistocene. These might have been inconspicuous physiological adaptations but two favourable behaviours that spring to mind are those that are likely to be most marked in *L. a. cyclotis*, tight family cohesion and co-ordinated threats.

Contemporary distribution of African forest elephant, *L. a. cyclotis* and *Elephas indicus* to illustrate role of tropical forests as refuges for elephants



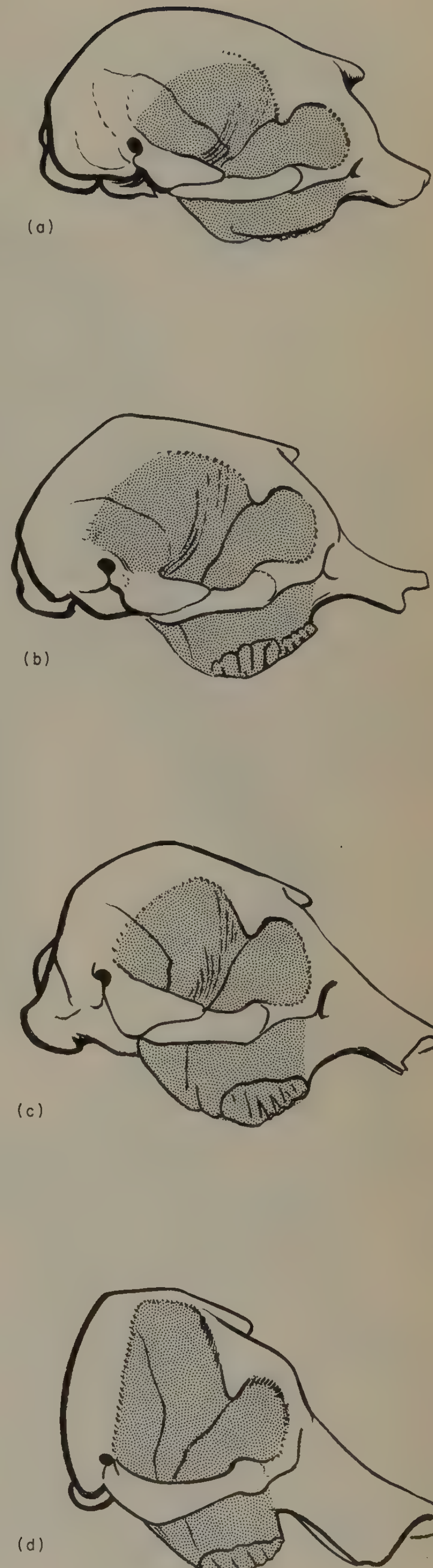
There are several possibilities. The last glaciation in the northern hemisphere saw the extinction of *Elephas antiquus* and *E. falconeri* and co-incided with the disappearance from the fossil record of the African *Elephas*. If drought, cold and human predation had exterminated *Elephas*, *Loxodonta* could have emerged from its forest refuges to fill a niche-vacuum of truly elephantine proportions. It is known that in about 12,000 B.P. warmer, moister conditions followed a cold, dry period that had reached its climax between 25,000 and 20,000 B.P. Amelioration of climate led to a great expansion of forest by about 8,000 B.P. (Hamilton, 1976) and this would have favoured the expansion of populations of forest dwelling elephants. Alternatively the emergence of *Loxodonta* into savanna could be related to an earlier degradation of forest or to the dry period that followed after 7,000 B.P. Several forest mammals appear to have adapted to woodlands, thickets and savannas following degradation of their habitat (see Vol. I, p. 78 and Vol. II) and forest elephants would have had similar incentives.

The re-emergence of *Loxodonta* into savanna would have been helped if desiccation following a major expansion of forest co-incided with particularly difficult conditions for their *Elephas* competitors. There is the possibility that *Elephas* suffered cyclic die-offs similar to those observed in contemporary African elephants. If wide-ranging climatic events precipitated a pan-African population crash for *Elephas* and happened to coincide with conditions favourable to *Loxodonta*, the latter's take-over might have been greatly facilitated.

This review of the elephant families' peculiarities can end with a brief consideration of the tusks. It has already been discussed in relation to *Loxodonta* how the relative size and orientation of the tusks can alter the position and proportion of other parts of the skull.

Drawings in this profile have shown how size, age, sex, race and species can have a bearing on the shape of skulls and tusks. There is also a great measure of individual variation and it is interesting to compare the morphology of tusked and tuskless elephants. The relative positions of the activities of the skull are altered in every case (opposite).

Facing page:
left column congenitally tuskless elephant (adult male); right column tusked elephant (adult male).



Changes in skull form from birth (a) to adult (d): (b) approximately 5 years; (c) approximately 8 years.

Elephant (Loxodonta africana)

Family Elephantidae
Order Proboscidea

Measurements

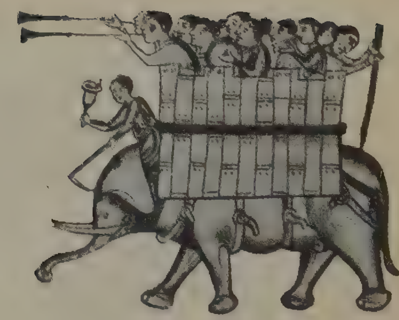
Loxodonta a. africana

height
3·2 (3—4) m males
2·5 (2·4—3·4) m females
weight
5,000 (4,000—6,300) kg males
2,800 (2,400—3,500) kg females
1,700 kg avge biomass weight

Loxodonta a. cyclotis

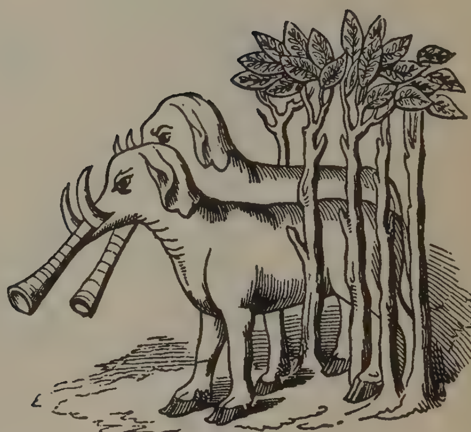
height
2·5 (1·6—2·86) m males
2·1 (1·6—2·4) m females
weight
2,700—6,000 kg (very few records)

Elephant (Loxodonta africana)



Local names

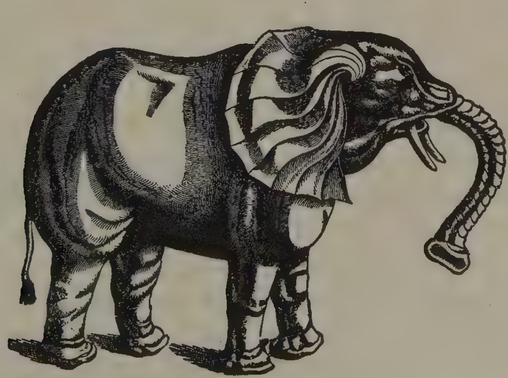
Ndovu, Tembo (Kiswahili), Njoru (Luganda), Njo'u (Kinyaturu, Lukonjo), Nzovu (Kisumbwa, Kinyiga, Kirabai, Kipare), Chovu (Kitaita), Ngori, Nzo'u (Kikamba), Njobu, Shofu (Kichagga), Yinjofu (Luhya), Injofu (Kijita), Nzogu (Kinyikamba, Kimaragoli), Njogu (Kikuyu, Kimeru), Njonjo (Lunyoro), Enjojo (Rutoro), Njogu (Lubwizi), Mbungu (Kuamba), Ezozo (Runyankole), Mhuli (Kisukuma), Ndembwe (Kihehe), Indembu, Oltome, Olkanchaoi, Olenkaina (Masai), Ltome (Samburu), Etome (Ateso), Embeliot (Kipsigi), Beliondet (Sebei), Belio (Kalenjin), Lea (Madi), Lyech (Lwo), Ewa (Lugbara), Araba (Kiliangulu), Morohdi (Somali).

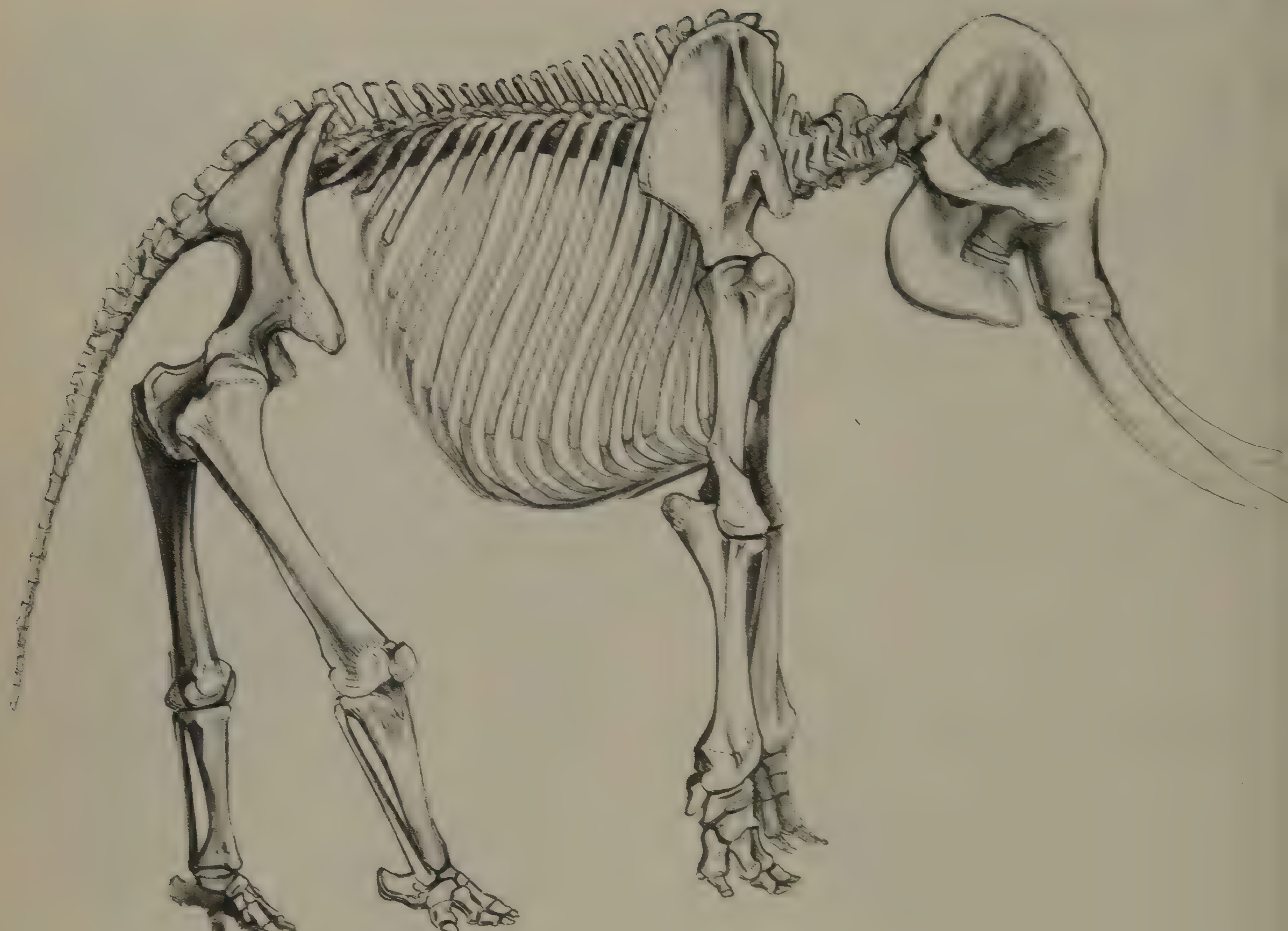


Races

Loxodonta africana africana	Bush or savanna elephant
Loxondonta africana cyclotis	Forest elephant

The elephant has always presented an interesting problem to authors and artists attempting to portray this extraordinary animal. Obvious and sometimes comical misconceptions could be expected in the iconography of peoples reconstructing the elephant from hearsay but quite fundamental misrepresentations can also be seen in the portrayal of elephants by chroniclers and artists who were clearly familiar with the animal but modelled their image on preconceived ideas. Thus it is common to find hocks and knees resembling those of ungulates, peculiar elaboration of the trunk, mouth, eyes and ears and an almost universal uncertainty about how the tusks fit into the head.

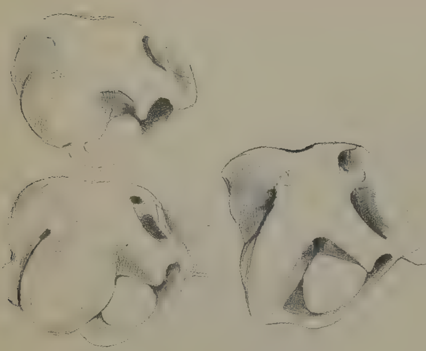




These misconceptions are due to the fact that almost every major structure of the elephant's body is specialized. Some of the numerous peculiarities can be directly related to the animal's great size. For example, the weight of the body has to be borne on limbs which are column-like. The enormous concentration of weight necessitates particularly massive bones which are aligned vertically. Notwithstanding its size and weight, the long forelimbs of the African elephant have great mobility, allowing it to keep the centre of gravity within the stride of its forefeet (one pace of which can cover a distance about two-thirds of the animal's shoulder height). The length of its stride is increased and energy is saved by a form of pacing that allows the hindfoot to occupy the place just vacated by the forefoot, so that the tracks of fore and hindfeet overlap almost perfectly in a pacing elephant. Both the radius and the ulna and the tibia and fibula are well developed and distinct bones, thus allowing the feet to achieve considerable rotation without loss of supportive

Loxodonta: carpal area.

strength. This mobility is partly due to muscular development of the lower limb, it helps the elephant to be an effective although careful climber of steep obstructed hillsides. Other features are related to gigantism in less obvious ways. Because the animal's bulk demands that at least three feet normally be kept firmly on the ground and, because weight bearing has put anatomical restrictions on their versatility, the limbs are correspondingly less wieldy in the animal's interactions with its fellows and surroundings. For these, the elephant relies more upon the head and its extraordinary appendages.

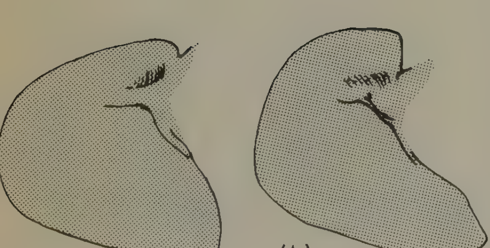


Surface modelling of the skull showing the development of cranial buffers around the brain capsule (still evident in the 3-month-old, top left).

The elephant's contact with its environment is mainly through its head, trunk and tusks. I have already discussed the relationship of a proboscis to cranial anatomy and touched upon the evolution of trunk, tusks and skull in the profile of the Proboscidea (p. 8) but some of the implications of size and weight can be imagined when antagonistic elephants bring their heads and tusks into collision or can be appreciated while the bole of an acacia flexes and cracks before pressure from a bull's broad skull.

The braincase of a mature elephant is surrounded by buffers of inflated bone. Pneumatization of the skull begins not long after birth, gradually to impose a distinctive and almost architectural superstructure over the ovoid cranium of the infant elephant. Because size tends to be the ultimate test of dominance, size is the feature most likely to be amplified in the ritualization of aggression and this is indeed the case with the enormous ears being used to full advantage in frontal displays. Elephant society, like many others, relies upon intimidation displays, which conserve energy and time and reduce the chance of injury. When spread, the ears follow the line of the forehead, which makes for the visual impression of a single rounded mass (see drawing). Furthermore, the greatest breadth is at the highest point, which ensures that the taller the elephant the more elevated his forbidding mass becomes. Display behaviour includes strategies to increase height and sparring elephants on a hillside appear to manoeuvre for the higher position; I have seen one make a slight detour in order to make its threats from the top of a low termite mound. All elephants try to get their head as high as possible when making a display, sometimes preceding this stance with smashing bushes and making upward scoops of the tusks, the latter accompanied by truly tremendous blasts of noise through the trunk and mouth. The display may take the form of a series of short advances, each one involving a shallow tusk scoop followed by standing tall with fully elevated head and ears. Although most of these gestures can be directed at one another, some of them with some frequency, elephants also drive off intruders and competitors by these means; the full display certainly frightens humans and other predators. What might have originated as intraspecific behaviour clearly benefits the elephants in more ways than one.

The ears have not developed their great size and mobility solely for display, although perhaps their exact shape may be influenced by visual considerations. The ears are a cooling device containing a rich network of blood vessels which are immediately beneath the thin skin covering the back of the ears. The fanning of the ears helps to cool the temperature of the blood through evaporation, which is often accelerated by a spray of water, mud or dust. Comparisons of the temperature of arterial blood arriving at the ear and venous blood leaving it have demonstrated the efficiency of this device.



Ear shape in (a) *Loxodonta africana cyclotis*: (b) *Loxodonta africana africana*.

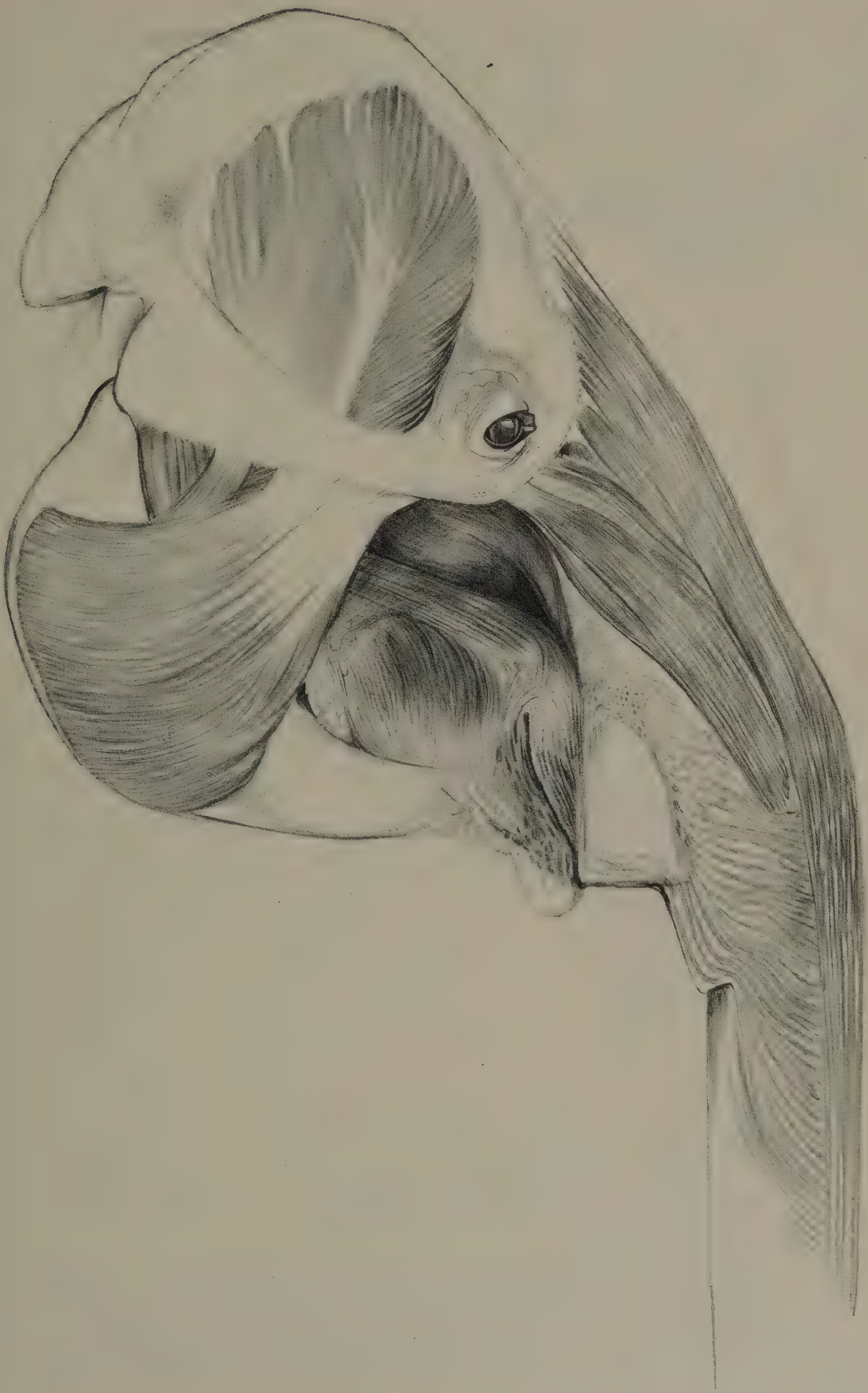
The ears of the large savanna elephant, *Loxodonta a. africana*, are distinguished by overhanging flaps along their upper edge. This parasol effect might be correlated with the greater exposure of the ear to direct sunlight, for this fringe is very much less developed in the forest elephant, *L. a. cyclotis*, which also has relatively smaller ears. Apart from its smaller size the forest elephant has straighter narrower tusks, the body has a more compact build and the forehead is borne further forward so that the tusks hang more vertically, a carriage that would presumably assist passage through dense vegetation.

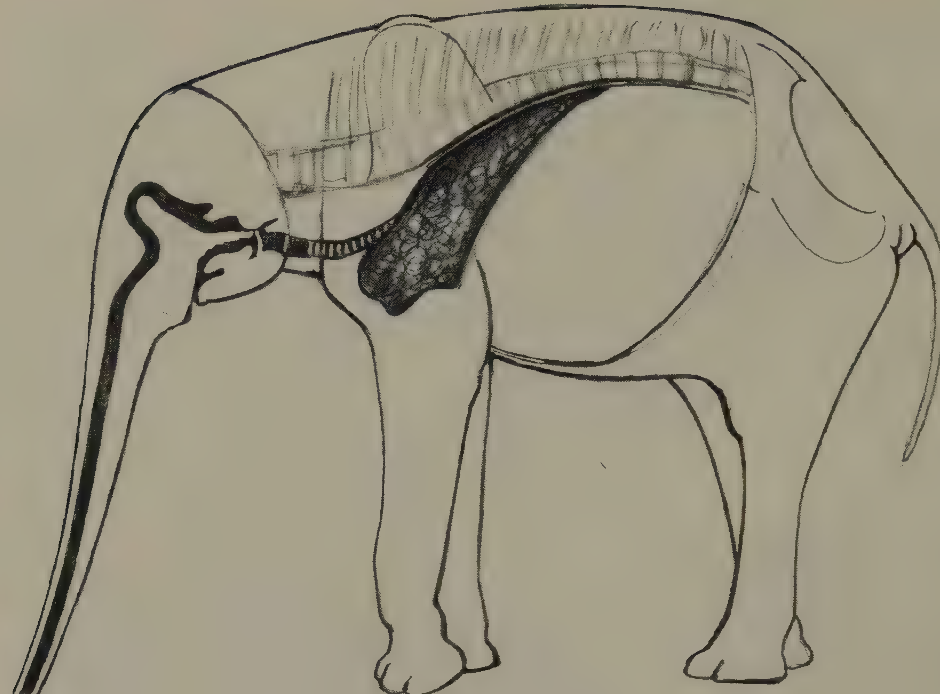
The ivory trade has its own jargon to describe different textures and colours of ivory and shapes of tusks. Some of these characteristics can be correlated with sexual, regional and ecological differences. Like other features, the tusk-shape is genetically controlled and because the basis of elephant society is the mother-family it is not uncommon to see a group of elephants which, in spite of different ages being present, show similarly shaped tusks. Thus a single group of sixteen elephants in the Rufigi area were all tuskless and in the same region a trend towards tusklessness or small tusks was said to be associated with particularly large ears and a rather smooth skin.

Tusks appear in some individuals earlier than they do in others but, in spite of considerable variation, growth is continuous and rather constant throughout life. Laws (1970b) has estimated that male tusks grow at about 11 cm a year and females 8·5 cm. Were it not for breakages many elephants would have mammoth-like tusks but they are put to use in even quite small elephants and heavy abrasion and breakages are often perceptible at an early age. The disposition of an elephant might have much to do with whether its tusks get broken or not; a case in point was the well-known elephant, "Ahmed" of Marsabit. This rather small male was known to be very mild and sedate which could have a direct bearing on the length and symmetry of his tusks if he had consistently refrained from clashing with other elephants or testing his strength against tree trunks and therefore avoided breaking his tusks (see drawing).

Living ivory is slightly flexible and a long tusk can sometimes be seen to bend very slightly when in use and the ends regularly snap off when stressed too far.

The evolution of the trunk was outlined earlier (p. 8). This enormous length of muscle with its two nasal tubes gathers in food by tightening a loop of trunk around a small mass of vegetation, breaking or pulling it off with a twist and then rolling it up to the mouth, where the mill-like molars grate the food briefly before it is swallowed. An average of four litres of water is inhaled up the nasal tubes to a height of at least two metres before being squirted into the throat, which is raised for each draught of liquid. The negative pressure created by this use of part of the bronchial tree for de-



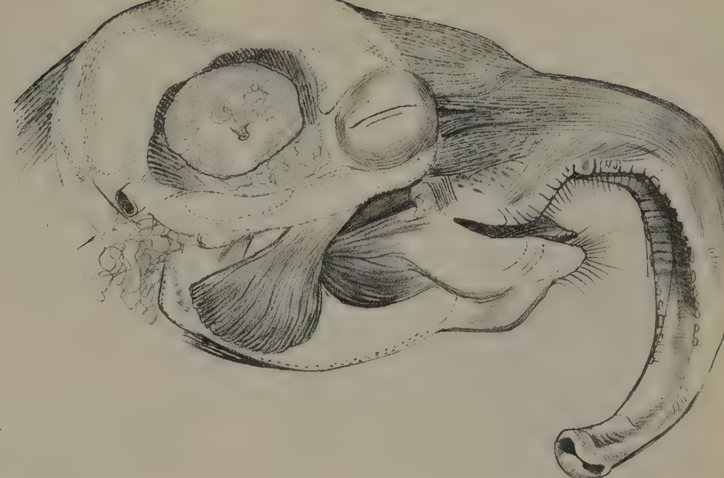


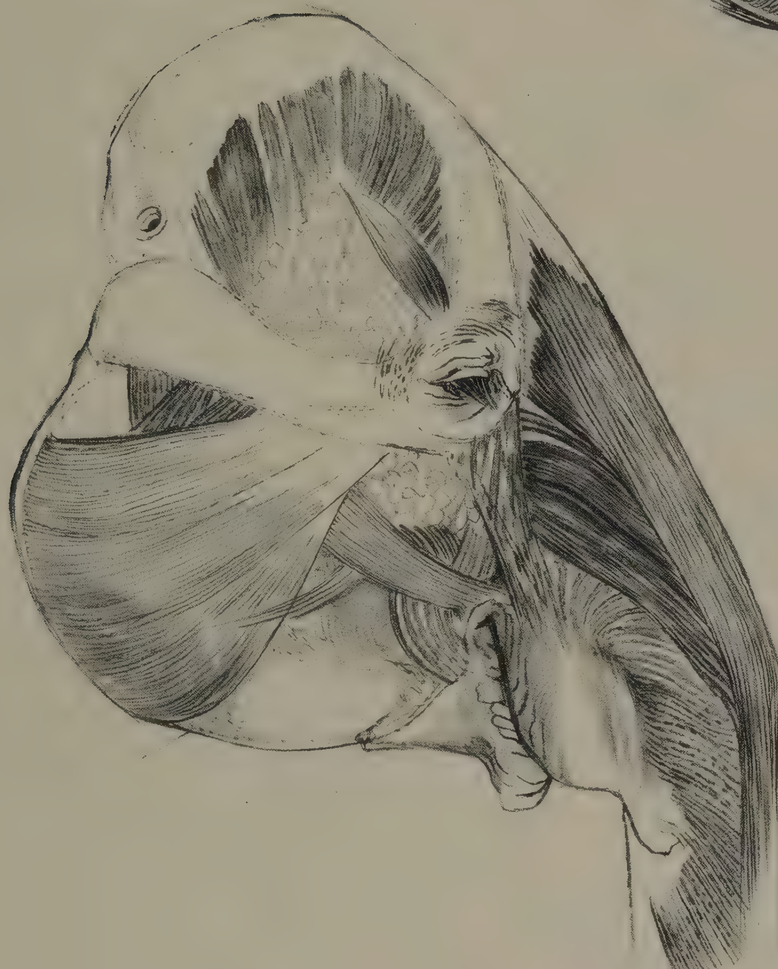
Lungs and air passage in the elephant.

canting water is probably the reason for elephants having lungs that are firmly attached to the chest wall and diaphragm (Short, 1964). Toldt (1913) pointed out that foetuses had normal thoracic cavities but that these were obliterated by the time they were born.

The trunk is also used as a sensory organ to both feel and smell objects, including the genitalia and temporal glands of other elephants and it is possible that it may be used to transfer and broadcast secretion from the gland to other parts of the body or to the surroundings. It slaps the young and may be used as a weapon against enemies. It is used to spray the surface of the body (particularly behind the ears and chest) with inhaled water, regurgitated liquid, mud or dust. Its position when seeking scents may be associated with particular situations and thus alert other elephants or serve to communicate information and might therefore have a signal function. The possible social functions of temporal glands are discussed shortly. Overlying the temporal muscle and immediately behind the eyes, they are derived from sweat glands and produce a strongly scented liquid secretion that sometimes dribbles down the cheek and into the corner of the mouth. Both sexes have them from birth but at the same time as the male begins his spurt of growth (at about 20 years) his gland also enlarges and may weigh up to three times as much as that of the female.

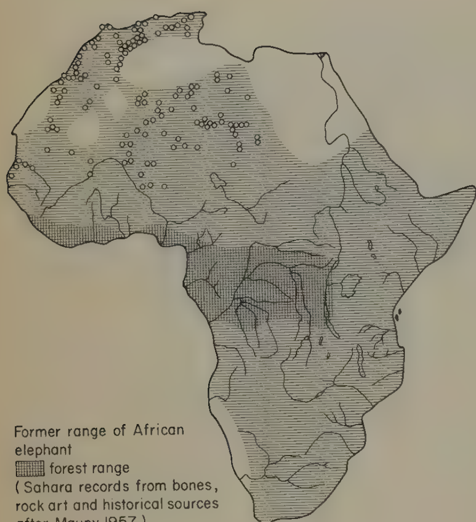
Other anatomical characteristics of the elephant are the possession of two pectoral nipples, abdominal testes and a simple, relatively small stomach with a very large caecum. There are several detailed accounts of the anatomy of elephants including Blair (1710), Stuckeley (1722), Cuvier (1849), Forbes





(1879), Boas and Pauli (1908), Eales (1926–28–29), Hill (1953) and Nielsen (1965). The earliest attempt at a scientific description of the elephant was that of Aristotle and there is no other African animal that has so long a record in history, nor is there any other species for which we have so complete a record of its past distribution.

Elephants were a favourite model for Neolithic cavemen, who depicted them in numerous sites across the Sahara up to 10,000 years ago, at which time the species extended over most of Africa from the Cape to the Mediterranean coast. Aristotle recorded that Egyptian Pharaohs had hunted or captured



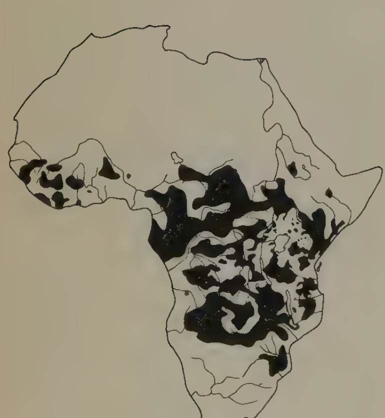
Former range of African elephant
forest range
(Sahara records from bones, rock art and historical sources after Mauny 1957)

elephants from the Nile Valley from early times and Egyptian artifacts of ivory date back 8,000 years. By the time of the Greek empire, Ptolemy II had to go further afield to capture elephants but they were numerous in Eritrea in 280 B.C. and many were shipped from there to lower Egypt. In North-west Africa the Carthaginians trained local elephants in the second century B.C. and Hannibal invaded Europe, crossing the Alps with 40 of them in 219 B.C. By this time the North African elephant population had long been isolated by the spread of the Sahara desert and it continued to decrease until its extinction by the sixth century A.D.

The final elimination of the North African elephant was perhaps due to hunting but it has been generally assumed that the disappearance of a rich mammal fauna from what is now the Sahara desert was due to a long term change of climate. However, Laws (1970a) has pointed to contemporary events in African parks as an illustration of how elephants can destroy all woody vegetation and thus hasten the deterioration of a fragile habitat. Rock engravings and paintings estimated to be 11,000—5,000 years old are scattered throughout the hills and mountains of the Sahara; many of these depict elephants, showing elephants were well known and perhaps common.

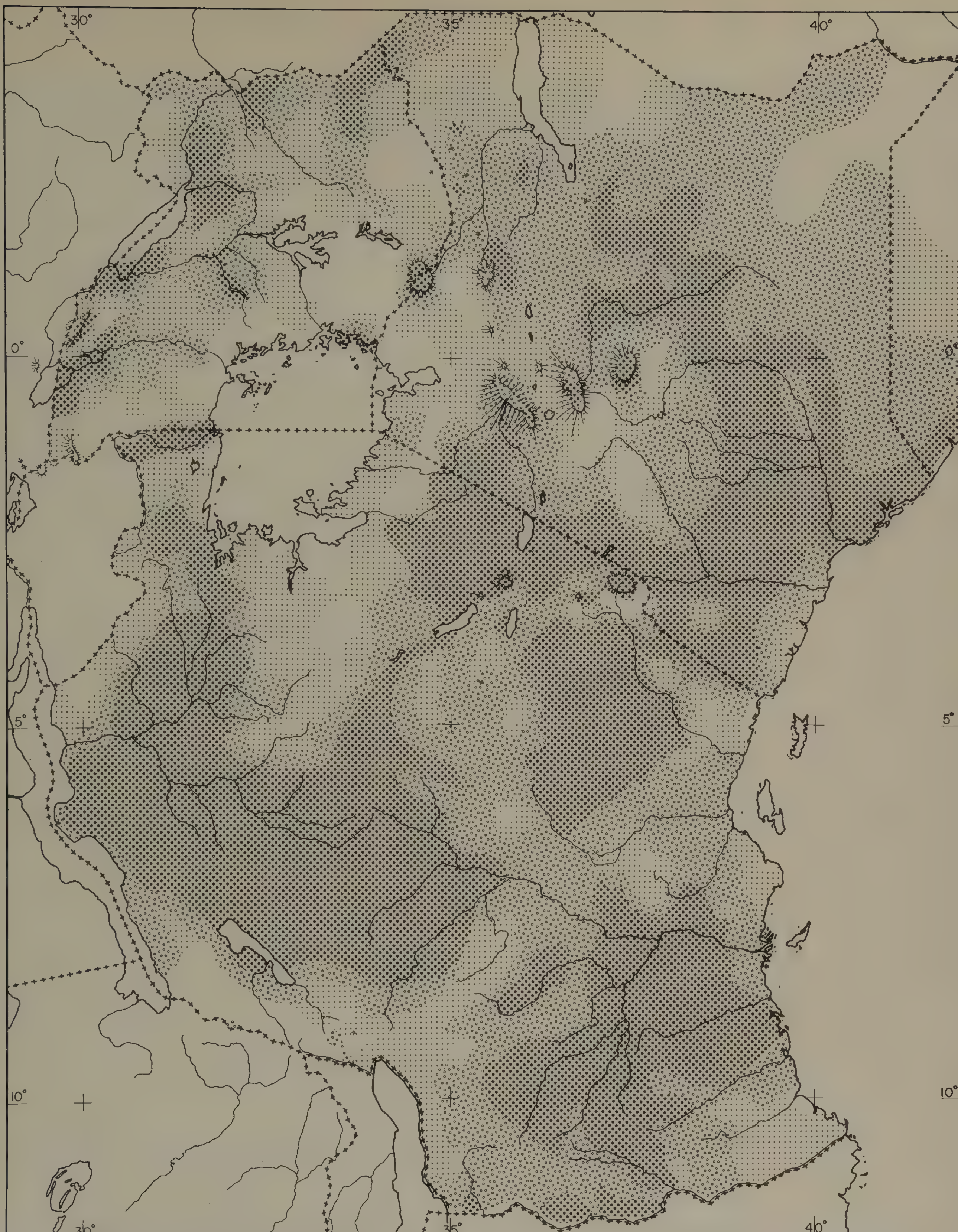
Both elephants and men might have contributed to the Sahara's becoming a desert but it was probably the drying up of the rivers that ultimately extinguished the elephants, for they are dependent on regular drinking.

Virtually all parts of East Africa are within an elephant's walking distance of water and there can be no doubt that the entire region was inhabited by elephants until relatively recent times. Here there are many areas where living memory and written records allow a detailed chronicle of the elephants' decline (and in some areas their multiplication). Areas with a long history of dense agricultural settlement have generally managed to keep elephants out, although occasional wanderers have continued to visit long-established cultivation from time to time. Such areas were relatively confined at the turn of the century and the earliest mass elimination of elephants in East Africa in this century was in Karamoja and Turkana, where the economy and culture of the people is based on cattle and a relatively small but widely dispersed population of pastoralists was offered the irresistible incentive of trading ivory for cattle. It was this situation that allowed W. D. Bell and other adventurers to make their fortunes in Karamoja in the first twenty years of the century. Today the high price of ivory and networks of roads have introduced fortune hunters into formerly undisturbed elephant areas and there is some uncertainty about the current status of elephants in many areas. A map of the elephant's overall distribution in East Africa today has little to do with the habits of elephants but much to do with the vagaries of the ivory trade wherever it is not a crude negative of human agricultural activity (see Volume I, p. 108).



Range of African elephant in 1975.

Elephants can find food in all vegetation types; hence their former ubiquity. Richer habitats will, of course, sustain more elephants and poorer ones fewer. Furthermore, individual elephants range over much larger areas if their food and water are widely dispersed. Elephants cannot afford to be very selective feeders, generally eating the plants that are immediately available and they are certainly less discriminating than any other herbivore.



Loxodonta africana

Without elephants by 1925

Distribution in 1975

Area in which eliminated since 1950

Area in which eliminated between 1925 and 1950

Miles

100 50 0 100 200 300

0 100 200 300 400

km

NB This map does not show areas where elephants were absent in 1925 and which have been colonized since

CLIMATE	ECOLOGICAL CONDITIONS	ELEPHANTS
DRY	Fires and destruction of grass	Move towards refuge areas Avoid fires and human activity
	Flood plains dry but grass still growing	Move on to flood plains Temporary concentrations in borassus groves
	Surface water finished	Move to hills, forests or rivers for permanent shade Less feeding. More resting Barking trees
Early rains	Flushes of green growth	Major movement initially by males Concentration on localized pastures, followed by dispersal
WET	Rapid growth everywhere	Longer feeding. More active
	Some valley soils gluey	Avoid slippery, sticky soils
End of rains	Grass long	Well dispersed in grasslands and savanna

The amount of food consumed by an elephant each day varies with the seasons but averages about 5% of the body weight and a mature elephant may therefore eat 300 kg in 24 hours. The stomach is relatively small but food can pass through very rapidly and meals are excreted 11—26 hours after being eaten.

In all the African savannas and woodlands grass is the most universally abundant vegetation in the wet season and therefore constitutes their main food at this time (Wing and Buss, 1970; Field, 1971; Gough, 1973; Guy, 1974). Burning of the grass in the dry season and the need for a more nutritous food and shade may drive elephants down into drainage lines or up into moister highland areas. These movements may be small-scale adjustments or they can involve major concentrations drawing elephants from a wide area into dry-season feeding grounds or refuges.

Because elephants range through a great many vegetation types and because they exist at very different densities, resident in some places, seasonal visitors in others, a very confused picture of elephant ecology and feeding habits has emerged. Because they eat bark, smash bushes and knock down trees, the effect of large numbers of elephants on woodland is dramatic and, if the elephants remain, eventually catastrophic for the woodland. Although it is an unspecialized feeder some foods are more highly favoured than others, such as the bark of *Faurea saligna*, *Chrysophyllum*, *Blighia unijugata* and *Dombeya*. It is, nonetheless, generally true to say that trees are attacked simply because they are there. The sudden appearance of new preferences (such as a taste for baobab trunks) might be a direct product of higher elephant densities simply making a more intensive impact on the existing vegetation. Nonetheless, some trees are actively avoided by elephants and others are not very highly favoured and these tastes have considerable ecological significance in most elephant habitats. For example, Buechner and Dawkins (1961) compared aerial photographs of the Rabongo Forest taken in 1932 with ones taken in 1956. They estimated an average reduction of 52% in the number of trees, but they also found that *Holoptelea grandis* had become the dominant species. *Guarea cedrata* and *Olea welwitschii* also benefit from being distasteful to elephants. In dry bushland, *Melia volkensii* and *Platycelyphium voense* derive similar benefits. In the Budongo Forest, Laws (1970a) reported that only 7% of *Cynometra* suffered damage by elephants while 36% of mahoganies and other commercially desirable species were damaged. He suggested that *Cynometra* forests might therefore represent a deflected climax induced by elephants. Such preferences extended over millennia must have exerted a major selective pressure on various habitats. Elephants having been widely distributed until very recently, we can expect many more examples of the elephants' influence on vegetation patterns to come to light as more detailed and careful studies on the preferences of elephants are undertaken.

The great size of the elephant and its crude feeding habits allow it to browse all but the taller emergent trees (these it may kill by ringbarking) and no acacia is immune, no matter how fiercely thorned. Because elephants are the only animals adapted to use such a wide spectrum of vegetation, their impact on trees is particularly conspicuous. The opportunistic nature of their feeding is sometimes masked by the rapid replacement of annual

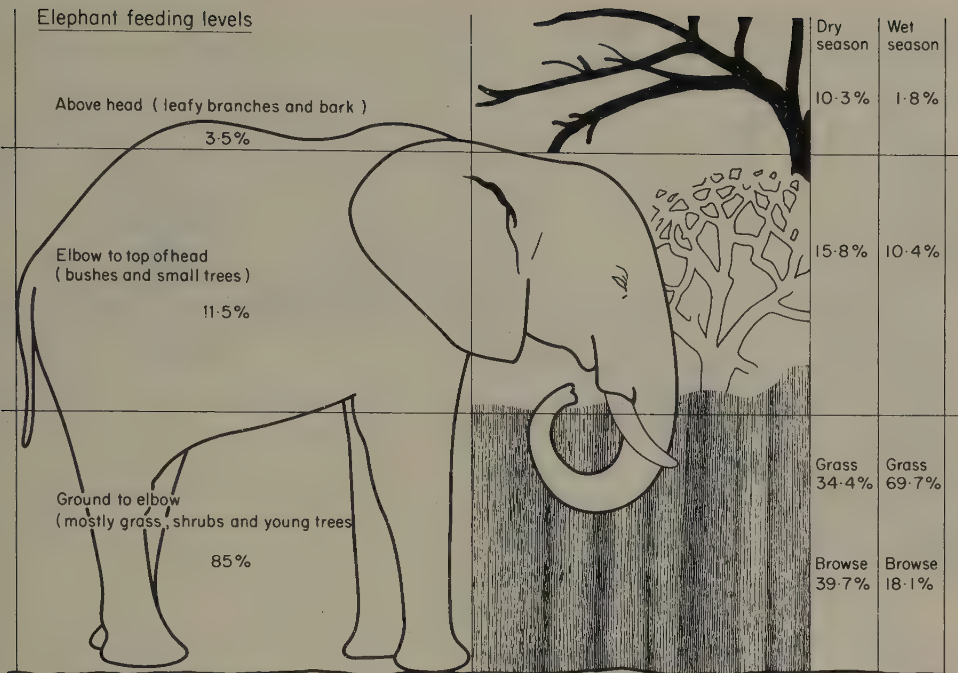
growth during the rains and by the activities of other herbivores and it is not generally recognized that elephants are probably competing to some extent with most other herbivores.

Since such a large animal must need quantities of minerals and other nutrients, several scientists have measured nutritional values for a wide range of foods. The inflorescences, new growth and bases of grass, herbs and browse are known to have generally higher value than mature or dry grass and elephants sometimes appear to select these, notably in the dry season, possibly in order to satisfy special nutritional needs (Napier-Bax and Sheldrick, 1963; McCullagh, 1969b; Field, 1971; Guy, 1974). Mineral needs are also met by visits to saltpans and licks and much earth may appear in the dung as a result. At the beginning of the rains when there may be a high proportion of soft green grass in the diet, bark might provide "roughage".

In the more extensive grasslands, swamps and marshes elephants may feed almost exclusively on grasses, sedges and herbs, but even in forest mosaics, woodland and savanna an abundance of grass provides the main wet season fodder. The herb layer is also the easiest level for the elephant to harvest, as the animal uses only the tip of the trunk to gather, twist or wrench off vegetation, conveying it up mouthful by mouthful. In the Ruwenzori Park, Eltringham *et al.* (1974) found that 75% of the elephant's feeding activity was at ground level. In North-western Rhodesia, Guy (1974) quantified the feeding behaviour of elephants; 85% of the food consumed was harvested from levels below the animal's elbow. In spite of this being a richly wooded habitat 70% of the wet season diet was grass, a proportion that dropped to 34% in the dry season, at which time browse became more important and there was slightly more feeding at higher levels (see diagram opposite). Elephants show signs of tiring when their heads are stretched up for any length of time and they seldom extend their trunks fully when feeding at high levels. They are more likely for example, to butt a fruiting tree and then feel around for the fallen fruit rather than pluck them directly.

Elephants eat many types of fruits and in common with other mammals and birds disperse seeds in their dung. It is a common sight to see seeds germinating in piles of old dung, which may contain over a hundred small seeds or several very large ones. Burtt (1929) listed thirteen species distributed in elephant dung in the Singida area alone, they included *Acacia*, *Adansonia*, *Balanites*, *Borassus*, *Grewia*, *Sclerocarya* and *Tamarindus*, some of which were excreted 16 km from the nearest bush. Other favoured fruits are *Rapanea*, *Ocotea*, *Datarium microcarpum* and *Hyphaene* spp.

The rank growth of vegetation during the rains easily meets the animals' nutritional needs and it is perhaps for this reason that few trees are damaged or knocked down at this time. Food is less easily gathered, is scarcer and more widely dispersed in the dry season. Furthermore, even in areas where there is still an abundance of grass in the dry season its protein content at that time, particularly in the coarse, fire-adapted species, may be totally inadequate to maintain a healthy elephant. Laws (1970) has correlated the delayed maturity, longer calving intervals and poorer condition (measured by kidney fat and height to weight ratios) of north Bunyoro elephants with their grassland habitat. McCullagh (1969b) has suggested that a dietary deficit in fatty acids may be the cause of elephants gnawing and stripping bark.



Percentages of food taken by Sengwa elephants (after Guy, 1974) classified by level, season and type (browse-grass).

It is often assumed that elephants push over shallow-rooted or weak-stemmed trees in order to get at the bark, twigs and foliage. The prevalence of this habit during the dry season, when these foods are important, would seem to support this. However, three-quarters of the trees are knocked down by males and a bull that is behaving in this way sometimes appears to be reacting to a social situation or some external excitement and may knock a succession of trees down without showing any interest in feeding on them, although females and young may hasten to eat the foliage which is now within easy reach. It seems possible that tree felling by males may be the elephantine equivalent of bush-thrashing or soil-horning by the artiodactyls; its value as a technique for bringing food within reach might be a subsidiary feature.

While the trunk is the main tool in gathering food, it is often co-ordinated with the feet and tusks. For example, the storage bases of grass tussocks are commonly eaten during the dry season. The tussock is held by the trunk and a scuffing kick breaks the roots away; after a swishing thump against the shoulder to sunder bits of soil, the whole tussock is eaten. Both feet and tusks can be used to break up earth or tree trunks, either to get at the roots or salty soil or to loosen bark. The trunk is used in combination with the feet to excavate water holes: during bad droughts these may be deep and need many hours to dig. Gordon (1966b) reported finding a deep trunk-made waterhole in a sandy river bed that had been plugged with a ball of masticated fibre.

This may have been the ruse of local hunters or an accidental occurrence but it could be comparable with other "covering up" behaviour (see p. 58).

Various pods, fruits or small rooted plants require to be handled by quite delicate movements of the trunk and circus elephants have been taught to pull corks out of wine bottles with the contents as a reward. In this connexion it should be mentioned that elephants in central Tanzania have been known to be attracted to homesteads by the smell of millet beer left outside to ferment in tubs. Likewise, fallen and already fermenting fruits of *Sclerocarya* often attract elephants. Drummond (1875) was only the first among several to speculate that elephants might be affected by a process of alchoholic fermentation continuing within their stomachs and there have been numerous descriptions of elephants behaving in a rather unco-ordinated way after feeding on ripe fruit. Some twigs, barks and fibrous plants are chewed for their juices and eventually spat out as dry balls of fibre. Some foods appear to be more thoroughly masticated than others and fibres of up to 20 cm may appear in the dung and I have seen quantities of 6 cm acacia thorns that were as sharp when excreted as when first swallowed.

In many habitats elephants are a major agent in the energy cycle; the daily consumption of a single elephant has been estimated to range between 200—300 kg and the production of dung to range between 140—275 kg, each individual defaecating ten to thirty times in twenty-four hours. Coe (1972) has studied the decomposition of elephant dung through beetles and termites and has also estimated that as much as 22% of the vegetation cover at Tsavo might be passing through elephants in the course of a year. It is often thought that feeding is continuous but in fact it is more in the region of ten to eighteen hours out of the twenty four and it has been shown that there can be considerable seasonal variations in the amount of time spent feeding (Guy, 1974).

The cycle of activity varies greatly from place to place and may depend

to a large extent on the degree to which elephants are hunted. In undisturbed parks small groups may even lie down and sleep in relatively exposed places at noon, whereas hunted elephants tend to gather in larger groups and enter very thick vegetation for a large part of the day, only coming out at night to feed in more open country. Tradition may be an important determinant of the activity cycle. For example, the Addo elephants in the Cape maintained their secretive and nocturnal habits for decades after official protection was enforced. Elephants usually sleep after midnight for several hours, sometimes standing but leaning heavily against one another or against a tree or else lying on their side. Before lying down they often scuff the ground with their feet first, and circus elephants commonly spread hay over the cold cement floors on which they may have to lie. The late night sleep follows a spell of intensive feeding from about 10.30 to 12.30. This midnight peak of activity has been noted in widely separated localities whereas the morning and evening feeding spells can be deferred, brought forward or extended according to the exigencies of the habitat, predation or season. Watering may demand difficult or dangerous journeys in some dry, semi-settled areas and in 1953—55 I followed elephants over 18 km from waterholes in central Tanzania that were only visited at night. A regular nocturnal drinking routine is followed during the dry season by elephants on the Galana (Parker, 1964). Likewise bathing and mud wallowing vary but wallowing, mud and dust-bathing are more conspicuous in the dry season. Elephants scratch and rub themselves a great deal, particularly after wallowing and bathing, and also on rising after sleep (Kühme, 1962).

Foetal lower jaw and tongue showing remarkable length.

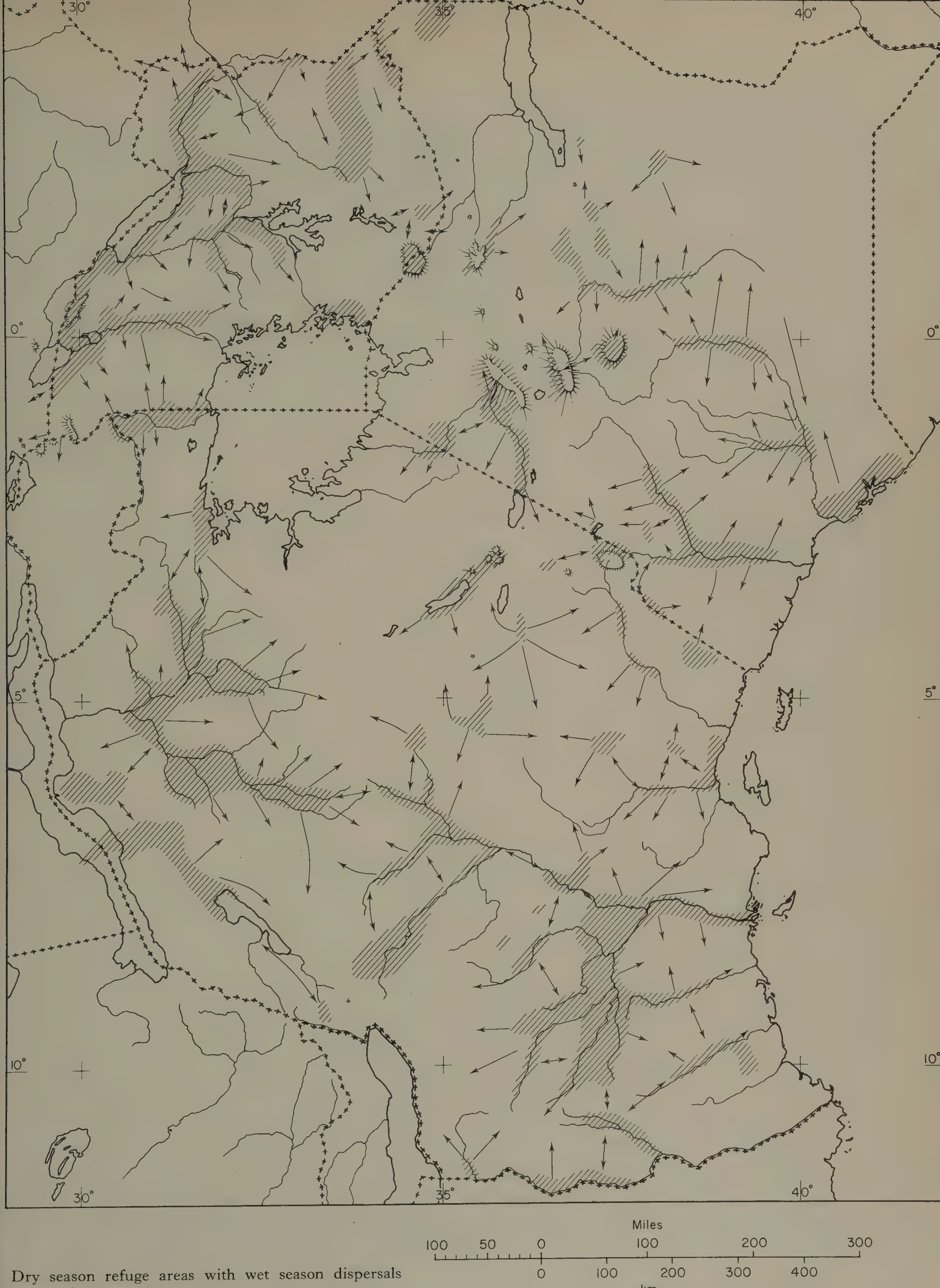
Diurnal activity generally drops during the dry season and elephants spend more of the day resting, preferably in some cool or shady spot. An abundance of food in the rains may be an inducement to continuous feeding while a severe scarcity or scatter of food may demand a longer search during the dry season. Forests and swamps have three advantages in the dry season. First, they are generally a source of green growth. Second, they provide relief from heat, shade from the sun and water and, finally, they may be a good refuge from hunters. Local conditions may make one factor more important than another, but the main dry season pressure on elephants is either to drive them into montane forests or along river courses and down into swamps. Widespread human activity and firing of the grass tend to reinforce this pattern and contract the area available to elephants at this time but in undisturbed areas where the resources of vegetation are well dispersed the elephants may also remain scattered. For similar reasons there is no single pressure that brings elephants together in large concentrations. It is common to find elephants converging upon stands of *Borassus* palms while they are fruiting in the dry season; furthermore, a year with a rich crop sees more elephants drawn together than one with a poor one, confirming that the animals respond well to the relative abundance of their food.

However, these gatherings are necessarily of very short duration for the resource that attracted them is soon used up. The natural sociability of elephants allows them to congregate in hundreds and this can be briefly advantageous for the exploitation of a concentrated but ephemeral food supply to get over a difficult period or, perhaps, to discourage harassment from predators; but there is no reproductive or other social incentive to

maintain concentrations which very soon destroy the vegetation. Yet prolonged concentrations have been reported with increasing frequency in recent years.

In modern times it is not only droughts that prohibit access to large areas of land, for expanding settlement has almost identical effects. Furthermore, the natural clumping response to harassment, particularly persistent contact with hunters and villagers, may also serve to counteract dispersal. In 1958 Buechner published the results of some aerial surveys in North Bunyoro which showed a distinct tendency for large herds to clump near or outside the boundaries of the Kabalega (Murchison Falls) National Park. This tendency was most marked in the dry season. Animals were generally more evenly distributed within the Park, most particularly during the rains when there was abundant food everywhere but there was no obvious dietary or ecological explanation for the clumping on the peripheries. Some years later Laws *et al.* (1975) recorded an average group size of 6·1 in the centre of the same Park but this rose to 22·5 on the periphery and they suggested that a breakdown or change in the behavioural mechanisms promoting dispersion was involved. Having its traditional seasonal movements restricted or prevented by cultivators, hunters and armed forest guards, this elephant population has been typical in responding to these pressures by concentrating instead of dispersing. Laws (1970a) pointed out that when small dry season focal areas (i.e. moist valleys or shady clumps of vegetation) are used by 500 elephants for 10 days the ecological impact is proportionately greater than when 50 use it for 100 days. Yet in North Bunyoro huge concentrations of very many hundreds of elephants have been observed to remain in an area of no more than 100 sq km for more than a month. Seasonal movements, dispersals and congregations are therefore likely to be the result of a complex interaction in which nutritional and physiological needs combine with strategies for security; to this should be added the element of tradition that may guide particular populations along paths learnt from the older elephants. The map opposite shows some recognized elephant refuges and the stipple indicates more extensive areas that have been recorded as being vacated periodically, particularly during dry seasons. Arrows indicate the direction of known movements but there is no implication that these are ancient migration routes; in fact some of them might be relatively recent corridors across settled land. At the present time both the dispersal areas and refuges are, in many cases, in the process of being settled by humans, fenced or managed for stock or for forestry.

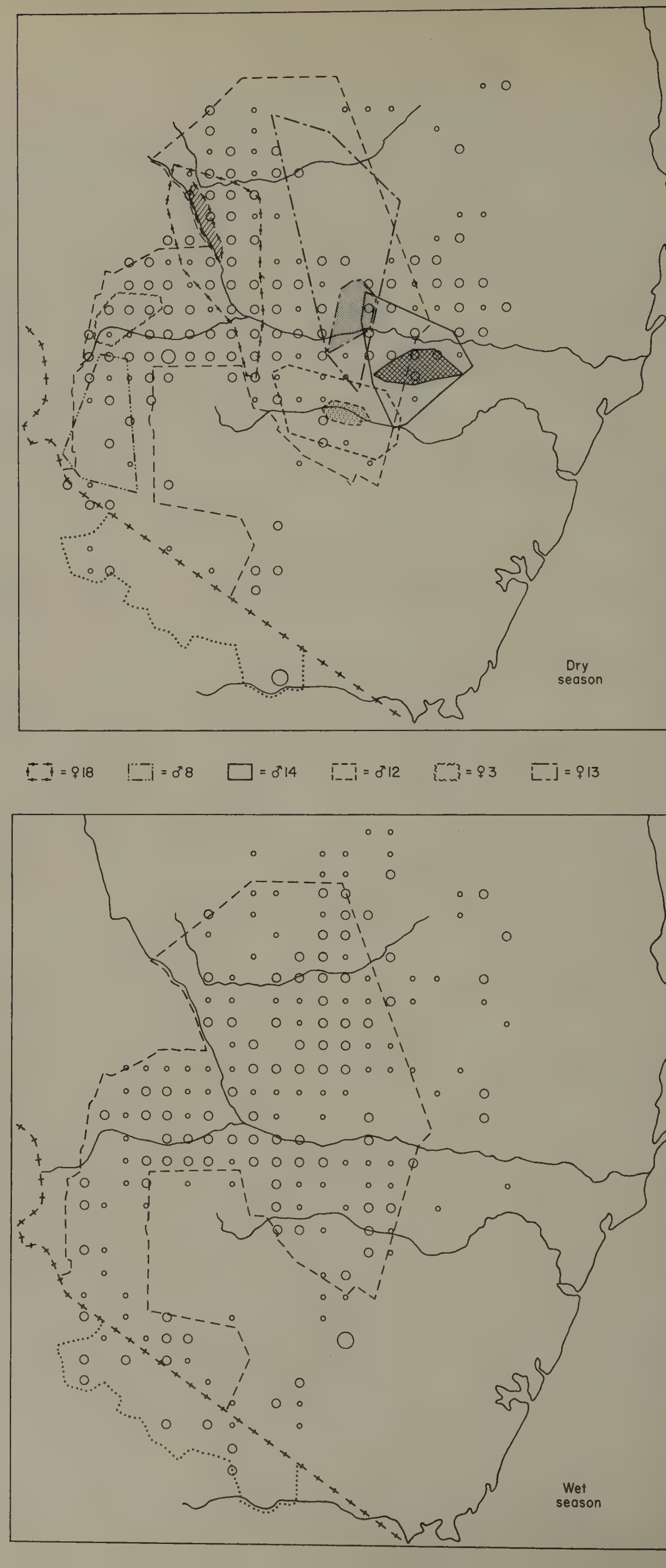
As early as 1890 Baker recorded shooting an elephant 35 km from the place he had wounded it six weeks before but the distances elephants move under duress are little guide to their range and it is only recent records from known individuals that have demonstrated the close relationship between range and habitat. A rich secure habitat can allow a home range as small as 14 sq km (Hamilton, 1972), while elephants in drought-prone East Tsavo can wander over an area as large as 3,120 sq km (Leuthold and Sale, 1973). The latter authors radio-tagged ten elephants and showed that the East Tsavo elephants responded fairly directly to localized showers of rain, benefiting thereby from flushes of new growth. In the better watered and more varied habitats of West Tsavo elephants had ranges one tenth the size and it was



Dry season refuge areas with wet season dispersals suggested by arrows.

The map summarizes knowledge of seasonal movements over the last 25 years. Elephants have now been eliminated in a number of areas shown here. (Data from Brooks and Buss, 1962a; Lamprey, 1963; Cobb, 1976; Uganda, Kenya and Tanzania Game Dept. records; and personal research.)

Elephant ranges in Tsavo and Mkomazi. Dry and wet season distributions after Cobb (1976), with home ranges of six individual elephants indicated. The dry season range of four elephants is shown in stipple (after Leuthold, 1977).



during their dispersal in the rains that elephants with quite different dry season ranges came into contact. Likewise in Bunyoro, Laws *et al.* (1975) have identified a small resident population living in the regeneration areas of the Budongo Forest, while at least three times as many elephants attempt to visit this refuge during the dry season, a movement that is strenuously combated by the Forest Department. Their arrival can be anticipated today from viewing platforms over 50 m up in trees and even massed herds are turned back by a team of armed hunters. It was this annual movement that Akeley (1929) described as the "biggest show I ever saw in Africa".

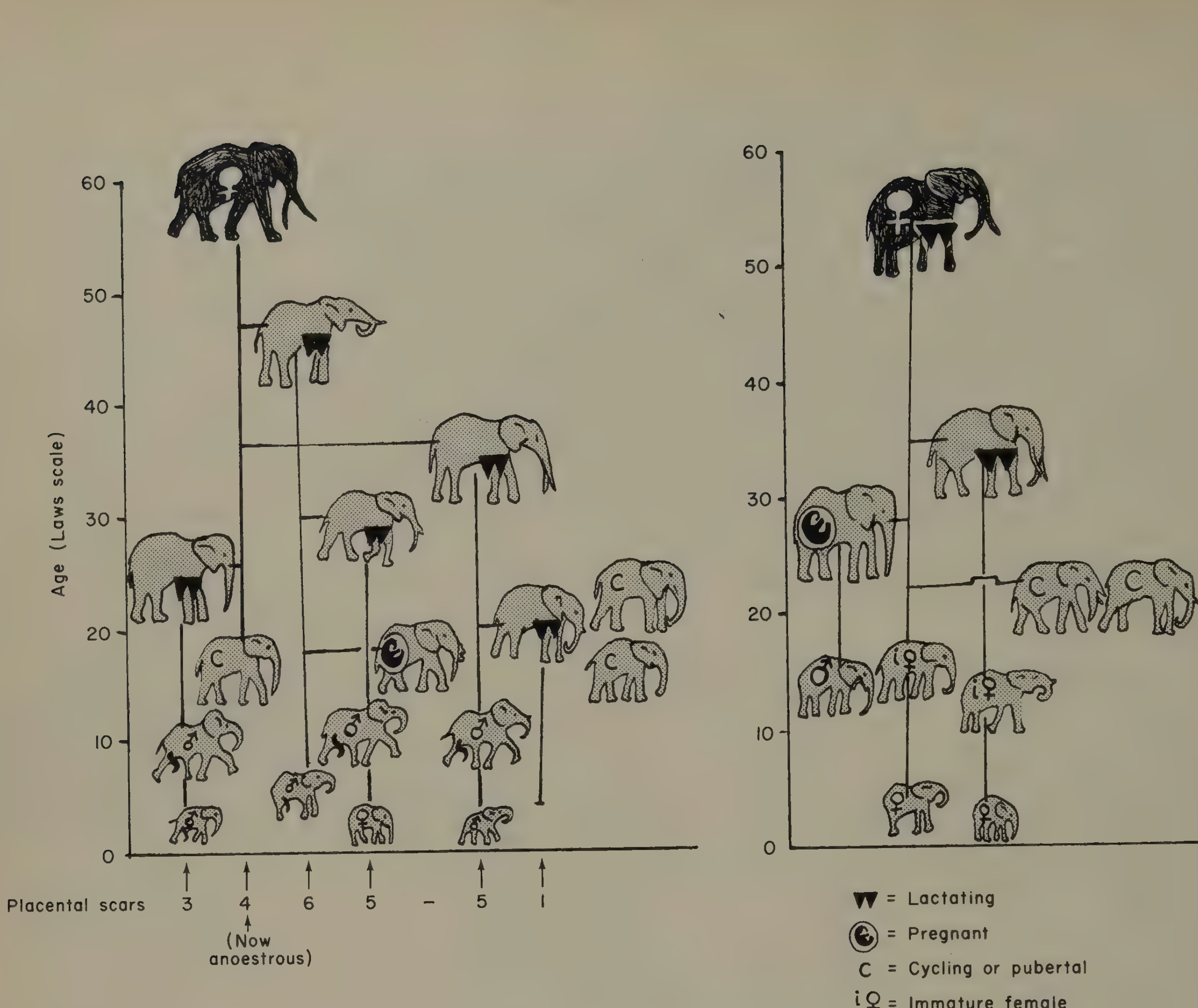
Considering these regional and seasonal differences and the variety of conditions under which elephants live it is no surprise to find great disparities in overall densities. The highest record is from the Lake Manyara Park, where a fairly self-contained population lives between the escarpment wall and the lakeshore.

The table below gives some recent estimates of densities for different areas.

Area	Elephant density per sq km	Source
Manyara National Park	5	Watson and Turner (1965)
Arusha National Park	3·3	Vesey–FitzGerald (1968)
North Bunyoro	1·9—3·8	Laws *et al.* (1975)
Ruwenzori National Park	2·5	Field (1971)
Ruaha National Park	1·1	Savidge (1968)
Kidepo	0·6	Ross (pers. comm.)
Tsavo	0·5	Laws *et al.* (1975)
Mikumi	0·26—0·43	Stephenson (pers. comm.)
Luangwa Valley	2·7	Caughley (1973)

The co-existence of resident and mobile elephants at certain times of the year makes it difficult to compare some of these estimates of density. To be meaningful such comparisons also need to be referred to the condition of the environment, carrying capacity and in some areas to socio-ecological factors.

The most detailed study of social behaviour to date concerns residential elephants living in the Lake Manyara Park (Hamilton, 1972). This park of 600 sq km has boundaries that are reinforced by the lake shore, a steep escarpment and recent settlement of farmers all around; there is, therefore, little movement of elephants in or out of the park now, although an aged and previously unknown wanderer was once seen by Hamilton. A year-long water and food supply allows individuals to live within small ranges and at a high density. Hamilton kept detailed records of associations over six years and on the evidence of group size frequency distribution suggested that the Manyara population could be subdivided into loose kin groups. These kin groups comprise related families, each of which is a stable matriarchy. The extreme range of ecological conditions in which various populations live, their very different dispersal patterns and the age structure of a local population probably puts limits on both the size of kin groups and the degree of



Two representative matriarchies with extrapolated relationships of family members indicated (after Laws *et al.*, 1975).

contact they can maintain at any given time. The fact that groupings of 200—500 elephants could be recognized from the air in Bunyoro suggested to Laws (1969—70) that these might represent a loosely associated group which he called "clans". In the absence of detailed knowledge of their ancestry or of the consistency of their association it is impossible to know whether such large groups are similar to the kin groups suggested for the residential Manyara herds. Parker and Archer (1970) demonstrated that regional populations showed consistent differences and Leuthold and Sale (1973) have revealed that elephants coming from different dry season ranges mingle together during the rains in Tsavo. The investigation of regional populations and their subdivisions remains a very promising area for future research. Apart from adult males, which have much looser relationships, all elephants belong to stable family units of about ten (2—25) individuals, which are generally led by an old female. This social pattern holds for all populations that have been studied (Buss, 1961; Glover, 1963; Shelton, 1965; Laws and Parker, 1968; Hamilton, 1972). Although elephants will congregate around any abundant source of food with a minimum of friction, the families are highly exclusive and the females tend to reject any stranger or "lost" elephant

that persistently tries to join them (Hamilton, 1972). This is a rare event however, as every individual keeps in close touch with its family by growling contact calls. If any alarm threatens, all members cluster closely round the matriarch and she determines which direction the family will take. When hunters kill a matriarch, the rest of the group will generally mill round and may try to lift her unless a second large female or a bull gives a lead in running away. When cropping teams shoot entire family units a distant straggler will even run towards the gun fire in order to join its fellows rather than run off on its own.

Although Hamilton was able to follow the development of several family groups over six years, it has not proved possible to document lineage. Relationships can seldom be deduced from observation alone because the younger females are more intensely "motherly" than the older ones and so closer bonds may form between siblings or other youngsters than between an older mother and her offspring. However, Laws *et al.* (1975) found that the age and placental scars of group numbers were so consistently spaced as to allow the reconstruction of family trees for nearly 60 families that had been shot in North Bonyoro during a cropping programme. The figure opposite illustrates two such families and their presumed relationships.

The oldest mother elephant usually maintains her position as leader of the group after she has started to decline in fertility (between 45 and 50 years) and, it is only when she is unable to keep up with the group that she drops out of the group. The rarity of solitary females suggests that senile matriarchs soon die off once they have reached this condition.

Hamilton has portrayed every female elephant living her entire life in a family group. This is either a process of gradually becoming more senior within her mother's own unit or else the unit may become larger than can comfortably forage together, in which case a split occurs and a new unit forms. However this is not a purely physical function of herd size.

When food is very sparse and elephants have to scatter widely, bonds between some of the too-numerous members of a large family may become difficult to maintain and the over-extended family may eventually break up into two groups. Hamilton was actually able to see this very gradual process take place and he suggested that group sizes were controlled by two opposing pressures, one being the tendency to aggregate in defence, the other being dispersal as a result of aggressive competition for limited resources.

Both food and water are cause for aggression between members of different families and within the unit itself. Not surprisingly relative weight tends to decide the outcome, but calves of senior mothers probably benefit directly from their protector's status and few elephants are intolerant towards young calves. However, weight is not everything and the position of an elephant with a hierarchy is perhaps also the product of inherited disposition, hormonal balance and tusk size, while the privilege of a high-ranking mother might also influence status, as has been demonstrated for several primate species.

Tusks may be used to prod rivals but their complete absence in some individuals might have a paradoxical side-effect on hierarchy. One might expect the tuskless elephants to defer to their tusked brethren. Instead, they have a reputation for being bullies; on one occasion Rushby (1953) was

watching a herd in the Lake Rukwa area feeding in open woodland. Twice Rushby saw a tuskless elephant sidle up to a young one as it drove one of its tusks into the bark to tear it away and scream loudly. Butting the young elephant, it drove it away from the tree. The tuskless elephant then took the broken bark in its trunk and tearing off a long strip, proceeded to chew it.

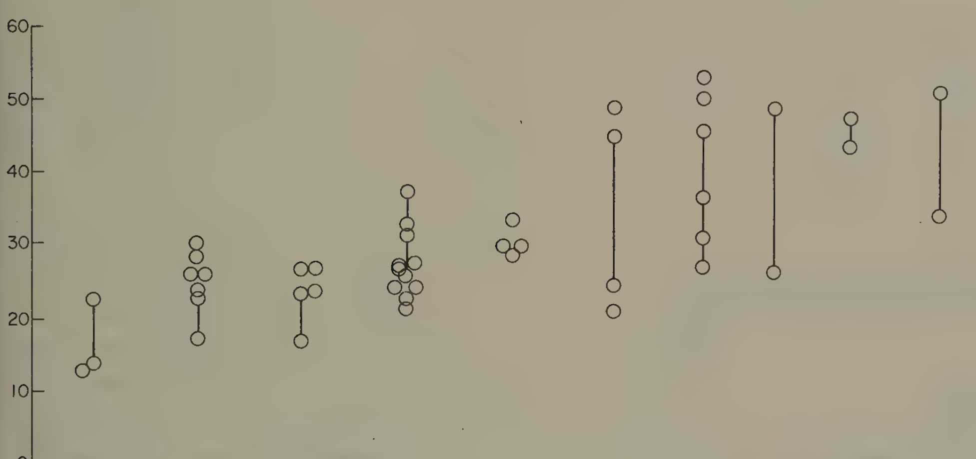
This incident illustrates that aggressive display and bluff play an important part in the elephant's natural history and this applies both within their own society and in relation to other animal species, whether they are competitors or predators. It also illustrates the direct advantages that are to be gained by hierarchy and how interdependence and mutual support under some conditions are not necessarily incompatible with members being competitive in other situations.

The literature and folklore that surround the disposition of elephants is immense. Most of it concerns the Asiatic elephant, since in Asia centuries of domestication and intimate contact with handlers gave a practical value to a classification of working elephants that recognized physical and temperamental characteristics (Sanderson, 1878). In an imperial culture it is not surprising that the names given reflected the caste-structure of Indian society but the implication of an elephant hierarchy is probably soundly based.

African elephants also have individual traits and Hendrichs and Hendrichs (1971) attempted to classify bull elephants into a succession of categories suggesting an explicitly linear status into which they were placed in virtue of the degree of sociability, initiative or fearfulness that bulls displayed while under observation. While much remains to be learnt about relationships between males, Hamilton (1972) has shown that associations both with one another and with families tend to be very loose in spite of their being social animals and in spite of the likelihood that resident animals in a confined area will meet up quite frequently.

Young males come into contact with males outside the family whenever herds gather together and they begin to associate with independent males long before the matriarch ceases to tolerate them. The actual age of expulsion probably coincides with puberty, which Laws and Parker (1968) estimated to vary between eight and twenty years. Hamilton witnessed the expulsion of a male approximately twelve years old and he radio-tagged males that had recently become independent from their parent family and which had entered into a highly mobile phase. Hamilton illustrated the ambiguity of the young male's status with an account of the herd's reaction when he immobilized such a bull, whereupon some of the family attempted to raise him to his feet while others attacked him; (however other interpretations are possible and of this more will be said later).

In North Bunyoro less than half the families were accompanied by bulls that were as old or older than the matriarch and were therefore unrelated to the group. The ages of adult males that were compatible with belonging to the family ranged from thirteen to twenty-eight (average twenty-one) years.



Age distribution (according to Laws Scale) of some male groups recorded in North Bunyoro (after Laws *et al.*, 1975).

The average age of bull herds on the other hand averaged over thirty years and a variety of different age combinations was recorded, including the commonly observed grouping of elderly bulls joined by one or two very much younger ones, a pattern that may be due to young males being mobile, exploratory but also sociable while old males are slower and more prone to be solitary, but nonetheless become a social focus for each passing bull. The tendency for bulls to have favourite areas is quite marked in some localities and Parker has seen an allmale herd of 144 in the Galana area. Bull herds larger than eleven could not be cropped in North Bunyoro because males, having weaker mutual ties to delay them when shot at, tend to rush off, each for himself, and family members are more likely to defend a fallen bull than vice-versa.

The degree of association between males and families may vary on a regional basis. Thus 75% of the families in Tsavo and Mkomazi had mature bulls with them compared with only 45% in North Bunyoro (Laws *et al.*,


½ grown ♂ howling after
being prodded by other md
group member is approached
by 2 younger ♀♀ & trunks
put to his mouth.

1975). Families are only drawn towards a bull when he has felled a tree or betrayed some other source of concentrated food. On the other hand, there are two main incentives bringing adult bulls into contact with families or kin groups, one being food or a waterhole, the other being oestrus, at which time it is possible that the female's hostility towards or fear of adult males might break down. I once encountered an adult female with her three well-spaced progeny of approximately three, seven and twelve years old. She was also closely attended by two large bulls. One of these bulls was shot, whereupon the second charged my party and was wounded. In the ensuing flight the lead was taken by the twelve-year-old and then the seven-year-old, followed by the bull, whose tail was held in the trunk of the matriarch (the youngest animal ran beside her). Whenever the male dragged his feet or staggered the female gave upwards butts in his hindquarters but after a fast run of over 7 km the bull was brought down with another shot, whereupon the female made a determined charge, from which she was diverted by the smoking cartridge, which was attacked with tusks and knees. After this demonstration the female ran off but the family returned during the night and pawed the bull's body. Protection of an adult bull by a matriarch is rare and, when observed by Buss and Johnson (1967), was taken as evidence that bulls could be true family members. Whether the female's protection of a bull bigger than herself was influenced by the demeanour of the wounded animal or by the likelihood that she was in oestrus is impossible to know. However, there is no evidence that such relationships are sustained; and the matriarch's behaviour may simply illustrate the strength of her impulse to aid a companion.

Many hunters have remarked on the elephant's habit of trying to raise a wounded or dead companion. The behaviour seems to be an extension of the family's protective concern; for new-born babies are helped to their feet, sleeping young are nudged awake and brought to their feet at the least alarm and the occasional bemiring of an infant in pot-hole tracks, muddy wallows or waterholes is generally attended by an excited cluster of young females, all attempting to pull the baby out with their trunks and forelegs.

The ambiguous reaction of Hamilton's female towards a young bull he had immobilized may be less a matter of their reaction to a young male than a generalized ambiguity or contradiction in the elephant's responses to a fallen adult elephant. In recent years it seems to have been a fairly widespread experience that an elephant's collapse elicits contradictory impulses in the immobilized animal's companions; occasionally the results can be fatal.

When a sick cow was darted in the Addo Park, a large bull and a cow came to assist her following an initial and momentary collapse. After a short walk together, the cow collapsed again, whereupon the bull turned and killed her with stabs behind the ear and temple. If one contestant in an elephant fight stumbles, the victor has been known to follow up his advantage with fatal stabs of his tusks so it is not impossible that the Addo male's reaction might have been brought about by an involuntary blow from the collapsing cow or by an equally involuntary aggressive gesture. For example, when a hunter in Tanganyika knocked down and stunned the larger of two bulls, the younger animal stood its ground, only to be violently attacked when the large bull got to his feet. After five minutes of combat with tusks locked the younger elephant was thrown and was then killed with several deep thrusts of the tusks.

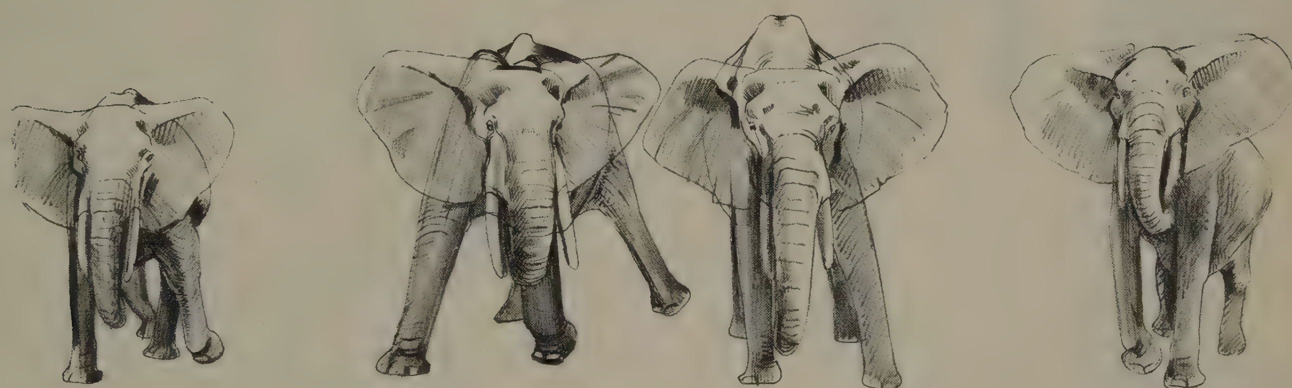
There are less dramatic but abundant observations of elephants reacting to carcasses. Here, too, an element of contradiction is apparent. The return of a family to the body of a fallen elephant and their scuffing at the body with their feet has been mentioned above. I have also seen an adult female make repeated visits to the brown skeleton of an older female, which had been shot several weeks earlier when she charged a team capturing her calf. This animal stayed by the body for quite long periods, swaying and pacing restlessly, occasionally pulling vegetation and tossing it in an aimless fashion and often scuffing the ground with her feet. The restlessness of elephants confronted with a carcass takes various forms. A grotesque illustration of the elephant's special interest in feet came from an elephant-cropping camp where the pads of slaughtered animals were skinned to make tourist trophies. During the night a herd discovered the rows of dismembered limbs. Although the sand-filled pads were enclosed by a well-wired enclosure, the wild elephants reached in, after which they kicked the trophies about with much agitated scuffing of the surrounding earth compound (Parker, personal communication). Sometimes scuffing at a dead animal's feet is followed by an interest in the tusks and more than one elephant has been seen to pull at a fallen tusk with its trunk, meanwhile standing on the other tusk. Occasionally pieces of a dismembered body or skeleton are carried for up to one kilometre and it is reasonable to suppose that this activity might be token "aid to the fallen", an explanation that is given added weight by observations of females carrying the decaying remnants of their offspring weeks after death (Bere, 1966).

However, when tusks are taken up they are sometimes deliberately smashed and it is possible that their symbolism as weapons may set up a conflicting impulse to that of carrying. The sight of a dead companion or its remains might very well trigger off conflicting impulses to attack, to give aid, and to flee or to stand guard. At low intensities these conflicts might find resolution in agitated scuffing with the hindlegs, some pulling at vegetation and even lifting up body fragments. More explicitly aggressive undertones are released when an excited elephant vigorously kicks debris back over a carcass or drops uprooted vegetation on to it.

A dominant elephant directs backwards kicks or foot scuffs towards a much smaller sparring partner; in captivity the gesture is employed at pestering humans or dogs, and at higher intensities elephants tear up or smash vegetation in an impressive intimidatory display that can be directed against both predators and rival elephants or, in zoos, towards dogs and the ogling public. Some individual elephants in national parks have gained notoriety by repeatedly tossing branches at minibuses full of camera-happy tourists. The common feature of all these displays is that the opponent in some way stands his ground and will not go away. The absence of any reaction from the source of aggravation generally leads to a closer and closer approach and heightening excitement may produce a progression from scuffing to kicking to branch breaking, uprooting and tossing. An interesting point about this sequence of actions is the possibility that it was originally an intimidating display that may have become ritualized into a sort of burial ceremony for objects that remain aggravating or disquieting in spite of being immobile.

There are numerous accounts of dead elephants being found under branches and other debris and also of lions and other predators being

covered in this way. Indeed, a well known Tanganyika farmer, Mr Stowesand, was but one of several elephant hunters who was killed and buried in this way by his intended victim,—his body was found covered with branches and leaves. Several species of large mammals smash up vegetation as part of their intimidation displays and the activity often suggests that aggression is re-directed. However, for the elephant this element can be obscured by the fact that it breaks so much vegetation in the course of normal feeding. Nonetheless, plucking and tossing without eating is commonly seen in situations of mild tension and it is particularly conspicuous in interactions between bulls. Confrontations are often across a bush or thicket and in the process of making rushes at one another, each opponent will scoop his head through the bush



before standing in the tall threat posture; sometimes one contestant will seize a branch or uproot a sapling and brandish it. Excited young males may rush about thrashing bushes or prodding at tree trunks in between bouts of fighting and it is smaller males in the presence of a larger opponent that are most prone to assault vegetation. Bush-thrashing sometimes slows down and graduates into tree-pushing, although the two activities are normally distinct. For the young male, however, they may be linked as different manifestations of re-directed aggression, the first belonging to the intimidation phase, the second to a symbolic pushing contest.

In a study of bull elephants in Serengeti, Hendrichs and Hendrichs (1971) found that immature and young adult males were the most prone to knock down trees. The crash of breaking branches seems to attract other elephants in the neighbourhood but the Hendrichs often saw tree-fellers pursued by higher ranking bulls. Large males, particularly those within a bull herd, show little interest in pushing down trees. On the other hand, solitary bulls, which are seldom in the younger age brackets, do it. It is not known whether a solitary condition might generate tension in a gregarious animal like the elephant, nor have observers in national parks always reckoned with the effects of their own presence, however discreet. As elephants are often attracted by the crash of falling trees and the sound of breaking boughs certainly carries better than an elephant's contact growl, it is even conceivable that a solitary animal may sometimes gain company thereby as well as relief from tension.

Very young elephants challenge one another with much head-nodding and shaking and by crashing through the grass followed by pushing contests or head-on butting. Both sexes engage one another in these mock fights almost as soon as they can run about and co-ordinate their movements, but the females generally lose interest in fighting by the time they reach puberty. Males, on the other hand, are particularly aggressive at this stage and are generally regarded as an unpredictable liability in zoos. Both within the family and outside it the succession of challenges and trials of strength continually tests each male's vigour and relative status. (It is perhaps the incompatability of such behaviour with the more orderly existence of the mother family that incenses the matriarch against maturing males.)

Before their tusks have grown, fighting youngsters entwine their trunks (the bases of which come together) and push rostrum to rostrum. At a later age they may clash foreheads, but this is rarer and the full ritual requires that the tusks engage one another, for without this the contest is merely a clumsy test of momentum and weight. With tusks and trunks locking the

heads together, the rivals try to throw one another off balance by repeated sideways and downward twists. The ritual is often quite phlegmatic amongst older contestants, with little indication of aggression and much squaring up and spreading wide of the feet before a bout of pushing. The long, often eccentrically shaped, tusks of older animals demand a more careful engagement if they are not to risk doing great injury to the opponents. A fast charge and a clash is less serious amongst younger elephants because the short tusks do not penetrate so far if they plunge into the head or body. Amongst older bulls the results can be almost immediately fatal as a long tusk with the momentum of a charge behind it may pierce the throat, neck, brain or heart of an opponent. Such deaths have been recorded and, in at least one instance, the victor had long straight tusks, a shape that is presumably particularly dangerous. Casualties are a reminder that elephants have ample capacity for killing and maiming one another but the rarity of deaths shows that ritual takes much of the danger out of bull confrontations. Females, which very seldom fight and so have no need for ritual, stab indiscriminately with their tusks when they expel young bulls or drive off a competitor at a waterhole. In the very unusual event of two cows standing up to one another the outcome may be more damaging. In fact, two cows that were once found dead after a fight had each been lacerated by the tusks of the other, and Parker (personal communication) found a cow that had died from multiple stabs.

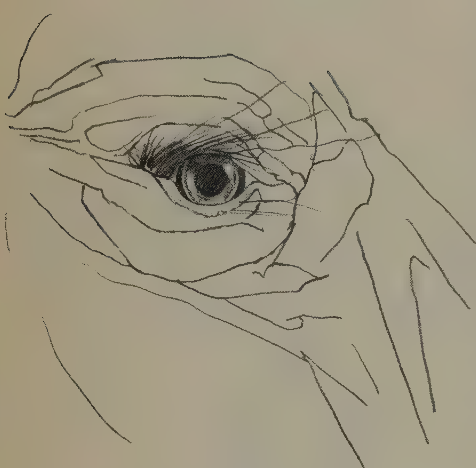
Submissive or vanquished animals, whether male or female, take refuge in flight or else spin about in a rump-presenting gesture. Because of the males' interest in females being largely restricted to oestrus, the gesture has an explicitly sexual connotation; among all-male groups it may also be followed by mounting but in their case it may be a characteristic of a situation where flight is impeded in some way, for mounting has been particularly noted as the finale to pushing contests when the opponents were within a large herd, in a confined space, or, on one occasion, nearly up to their necks in water (Shelton, 1965).

At any stage in a contest the inferior elephant may put the tip of its trunk up to its opponent's mouth (a sign of submission in many more contexts than just fighting). It is also likely to hold its head lower, draw its ears back and curl its trunk more tightly. The superior elephant, in contrast, carries its head higher, extends and flaps its ears and may bring its trunk forward and touch the other on the side of the head. The latter gesture might allow the temporal gland to be smelled and Kühme (1962) has illustrated a young captive feeling its own temporal gland just before coming into contact with an opponent. This gland produces a rich flow of apocrine secretion whenever the animal is excited, particularly in social situations or in alarm. For an individual the secretion may be a simple "extension of self"; its scent could possibly have a reassuring effect when broadcast on the air or transferred to the environment or on to other elephants by direct contact. That it allows elephants to recognize one another as individuals and reinforce the recognition of age and sex seems very possible. Should the individual's hormonal balance have any influence on the gland it could perhaps help in their assessment of one another's status. Hamilton recorded 90% of the females at Manyara as showing signs of secretion whereas only 54% of the males did, in spite of the fact that the males have glands three times the size (weighing in the

region of 1·6 kg). This disparity in the flow of secretion may be due to the greater need for family members to keep in touch with one another and these difficulties could be compounded by a high population density. When the Manyara elephants were compared with more sparsely distributed populations, the incidence of actively secreting glands was seen to be much lower. Hamilton saw a sudden flow of temporal secretion during threat displays and amongst members of a group after a cow had fallen and the contagion of excitement in a group finds immediate expression in a strong flow in almost all members of the family.

The more herds come into contact, the more important individual recognition becomes. Together with the voice, the strong smell of the temporal secretion might help members of a family to meet up again after temporary partings. Their olfactory powers are astonishing, individuals can trail each other down by simply following one another's tracks.

I once came upon a family of elephants walking in single file up a woodland path; being on their own path, I withdrew downwind to watch them go past, but at the point where I had halted, the matriarch leader made a slight scooping motion with the tip of her trunk in the dust and immediately turned to follow my most recent footsteps with pointed trunk held close to the ground. As she came on, she gave a wheezing squeal and flapped her ears but it was clear that she could neither see nor hear me and was displaying purely on the evidence of the fresh scent left at my passage or by my shoes.

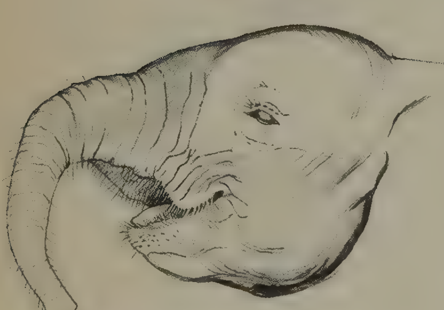


Detail of elephant eye.

Scent is evidently their most highly developed sense, although they can hear well and have fairly good eyesight when the ground is open and the contrast is good. I was once surprised to be the object of an elephant display while still at a distance of over 200 metres and realized that my moving silhouette must have appeared for a moment against the skyline; they are normally unable to distinguish a figure at that distance when not guided by scent or sound. Indeed, they can be approached very closely when cover is good and the wind right.

Scenting with the tip of the trunk may be closely allied with the sense of touch and this is especially true of young elephants. As a child I had a brief but intense relationship with an orphaned infant and vividly remember the persistence of its probing, snuffling trunk tip as it felt my ears and nose or pushed at the corners of my mouth.

Males test urine and faeces and also the female genitalia with the trunk and then bring the tip up to their mouth. Hamilton suggests this gesture may bring scent to the well developed organ of Jacobson in the roof of the mouth and may be the equivalent of *flehmen* in ungulates.



Elephant foetus showing vibrissae around mouth and trunk.

The principal means of communication is by sound, the commonest noise being the deep growl with which members of a family group keep in touch. Each individual probably has its own signature growl by which it can be distinguished and Hamilton saw two adult members of a family unit exchange loud calls when they became separated within an assemblage of a hundred odd elephants.

The matriarch often emits the loudest growl and she responds readily to calls from straying juveniles. (Indeed, all members of a herd will rush to the aid of an infant uttering distress calls. Even half-grown juveniles may elicit protective responses and I have seen group members approach a youngster

that had been prodded by another elephant and put their trunks to its mouth in response to its bellow of pain.) On a windless day growls will carry for nearly a kilometre. All classes seem to greet one another with a growl when they meet. The noise is not made by the bowels as is sometimes thought, like trumpeting it originates in the larynx.

Displays against intruders are often initiated with an ear splitting blast while roaring and squealing may accompany fights. An elephant hurt in a fight may bellow (but bullet wounds are generally sustained in silence). The distress squeals of baby elephants elicit immediate interest in adults. Adults have a muffled alert call which has been described as a gurgle or soft deep "broomp", which is followed by a silent and rapid decamp.

Apart from the auditory and olfactory clues, elephants evidently respond to one another's body postures and attitudes. It is sometimes difficult to distinguish between postures that are incidental to an activity and those that might actually serve as visual signals. As I have already remarked, the shape of the extended ears is probably an important part of the intimidation display and the extended or curled trunk implies greater or lesser confidence, as does the raised or lowered head. That elephants may watch others very carefully for visual clues was borne out by Mitchell's (1963) observation of a small herd with some very young calves which stood at the edge of a thicket one hot afternoon, watching two bulls that were cautiously reconnoitring a waterhole some 400 metres ahead of them. The moment the bulls adopted a relaxed posture the herd ran to the water. Because the bulls ignored the water, synchronized their postures and both stood facing the group of females and young with limp trunks and ears flat to their sides, Mitchell had the impression that a visual signal had been used.

Normally signifying submission, flattened ears in a bull may instead be a means of reassuring inferiors. Rather than relief from an imagined external threat it may have been a direct reassurance from the bulls that elicited the females' prompt response.

It would be interesting to know more about the role of sight in the elephant's communication system but however well developed it may be, it is strictly subsidiary to scent, sound and touch, a fact that is borne out by the occasional reports of blind but apparently healthy elephants. In fact, one such animal, a wild cow in Tanzania, was reported to be deaf as well and followed the movements of her calf in every detail.

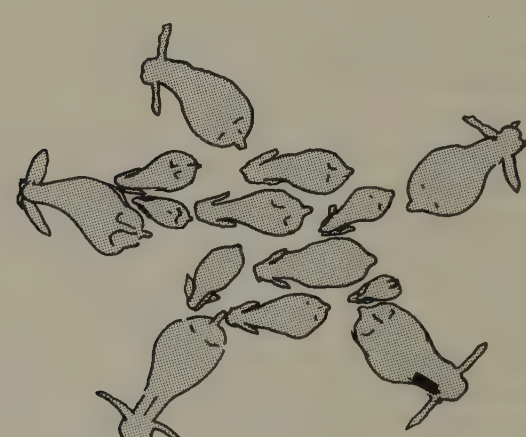
As was remarked earlier, various interactions are characterized by the level and angle at which the head is carried. Gaits, too, are altered by the relative position of the head as well as the speed of pace. In general, the head hangs relaxed while the animal rests, forages or walks slowly. If elephants set out at a fast pace, as they can do when water is at some distance from their feeding grounds, the head is raised higher and the speed may range between 10 and 16 km per hour. When an animal is excited, the head is raised very high (and the ears are also pitched up at an angle) and over short distances a charge may reach 35—40 km per hour. When climbing, the animal moves cautiously, testing and compressing its foothold before taking its weight. Elephant paths generally follow good gradients and in really mountainous areas tend to run along ridges. When descending they avoid overbalancing by sitting on their buttocks or they come down sideways or backwards.

Accidental falls over cliffsides have been recorded and panicking elephants over cliffs used to be a hunting technique in some areas. When unable to reach fruit, branches or stratified salt deposits by any other means, elephants rear up on their hindlegs (a favourite stance for circus animals) and both Pienaar (1967) and Parker (pers. comm.) have seen aggravated elephants rear up on their hindlegs in order to reach out for a helicopter hovering overhead—an interesting elephantine response to aerial predators!

In deep water elephants can either swim or walk with only their trunks above water. The latter was once seen in Lake Rukwa, where the elephant was beneath the surface for a distance of over 7 km bringing its trunk to the surface only in order to be able to breathe.

Both *Loxodonta* and *Elephas* are active swimmers even in the ocean. The latter species has been recorded going for six hours without touching the bottom and Hannibal's African elephants as well as crossing the Alps had to swim the Rhone and other rivers on their way to Italy. Elephants carried over rapids have been found drowned but such accidents are rare.

Of all aspects of the African elephant's behaviour, the one that probably insulates them most against other species, whether predators or competitors, is the intimidation display. When single opposing elephants indulge in this noisy and dramatic contest, the commonest outcome is for the less confident animal to flee and the same outcome is usual with a predator. If he stands his ground after one charge, the opponent usually tries another rush and any advantage is likely to be pushed home. The size of the elephant and the volume of noise it produces are enough to frighten most predators; likewise, other animals will scatter from a waterhole if an elephant starts a display.



Elephant group clumping defensively.

Effectiveness is enhanced in family units by all the larger members bunching together and trumpeting and shaking their ears, meanwhile scooping and tossing their heads in a series of short advances, which are sometimes closely synchronized. A feature of these group defence movements is the tight packing of the larger members around the matriarch and heavy leaning against one another while continuously reaching out with the trunk to touch one another, particularly in the mouth. It seems that the support of an ailing or wounded member is but an extension of this mutual support behaviour

and the combination of outward aggression and mutual conciliation (i.e. trunk sucking) is striking. During these demonstrations the younger calves often get in among the legs of the larger ones but face away from the source of disturbance; when the defence formation is circular these youngsters tend to cluster facing into the centre, while the elders face out around the periphery.

After a display, tension declines slowly and the elephants continue to weave from side to side, peer over their shoulders with raised or jerking heads, throw up dust and slap vegetation against their sides.

Although charges are occasionally followed up it is more likely that a serious charge is made silently and without preliminaries. Most such attacks take place in overgrown habitats.

While humans have probably been the most important predators for many millennia, the larger carnivores do kill the young from time to time and lions have even been recorded killing an adult male (Melland, 1938). A seven- or eight-year-old elephant killed by lions in Tsavo had lost a section of its trunk and sustained deep wounds on its shoulders, legs and neck in the prolonged struggle that preceded its death.

Hyaenas have attacked young elephants, and elephants have been seen to display against wild dogs, which suggests that they also might harry the young occasionally.

An elephant drinking in the Nile was once seen to be seized in the trunk by a medium-sized crocodile. The reptile was pulled up and thrown out of the water while the elephant ran off, an incident that suggests that these reptiles might be rather undiscriminating about their prey. In 1953 I found the crushed remains of a 5 m python lying on the hard sandy floor of the Issaua River. The dry river bed had a series of pools along its more sheltered reaches and at the margin of one of these pools the snake's progress could be traced from a dense evergreen tree across the open sand. A unit of four or five elephants with a young one among them had come to the pool, and one of them, using its feet only, had trampled the snake's head and some of the body into a pulp, tossing small pieces of it aside. Whether the snake made any attempt at attacking an elephant or whether it was simply there and was itself attacked could not be ascertained in spite of the evidence being only a few hours old when I found it.

Waterholes are often the site of fights between bulls and minor competitive squabbles within groups, and this truculence is often directed at other species of mammals. Rhinos sometimes threaten or are driven off and there are several records of elephants driving off and also killing lions, buffaloes and warthogs at watering places; also, a bull eland and an oribi have been reported killed. However, it should be stressed that attacks on other animals are highly unusual.

Competition around a waterhole cannot be compared with competition over vegetation between elephants and other herbivores. Elephant feeding and trampling favours some species but in times of shortage competition can be serious for large species like the rhino, which also have bulk needs. In Tsavo rhinoceroses have been particularly affected during drought years with both species finishing all the edible vegetation near the river, and the rhinos having a shorter range, dying first.

When elephants die from starvation, their deaths are often hastened by disease. Nutritional deficiencies and heat stress probably increase an elephant's susceptibility to a variety of diseases, including cardiovascular conditions such as arteriosclerosis and atheroma. McCullagh (1969b) has demonstrated that diseased elephants in North Bunyoro were suffering from nutritional deficiencies. However, a popular mythology has arisen around the supposed behavioural stresses of elephants in national parks in which the frustration of so-called migrating instincts has been invoked to explain disease and "wanton destruction" or "vandalism" of elephants against trees (Sikes, 1968).

Diseases and parasites that have been recorded from elephants are listed in the Appendix (p. 346). They are the only hosts for a species of botfly which passes its larval stage in the soles of elephants' feet. Anthrax is often fatal for elephants and has even infected an ivory worker as well as a zoo keeper cutting up a contaminated carcass.

Occasionally elephants are the victims of accidents, such as being struck by lightning, pinned by falling trees, bitten by snakes and apparently being poisoned by the fruit of the arrow-poison tree, *Acocanthera friesiorum*. One accidental death was the result of choking on a large bees' nest which was found in the animal's throat. Fire has been invoked as a common hazard in grassland and the practice of ringing a herd of elephants with fire is often recorded as a traditional means of maiming them. There have also been sightings and photographs of individuals reduced to walking on the exposed bones of their digits, after the skin had been sloughed off. However, fire is a normal feature of their environment and seldom elicits great excitement in elephants. Indeed, Parker (personal communication) has watched elephants walk through burning grass without being forced to do so.

In Uganda, an aggressive female actually trampled out a grass fire that was lit to deter her from chasing people, a circumstance which would suggest that the elephant may have treated the fire as she would a small predator.

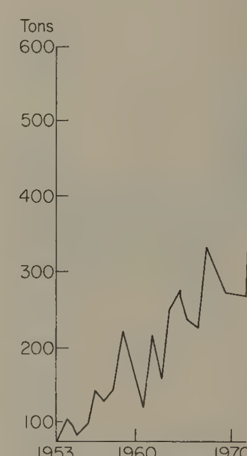
The most important predator of the elephant for several thousand years has been man. The hunters have for the most part been Africans but the incentive to kill for ivory has come almost entirely from outside this continent, from the Far and Middle East and Europe. The wealth of the old coastal cities, Zanzibar, Bagamoyo and Mombasa was derived from trade in ivory,

timber and slaves. This commerce penetrated deep into eastern Africa to reach all the major concentrations of elephant populations and when slavery was suppressed by Britain, the established network of communications with the coast continued to be used for the ivory trade. In many remote areas in the heart of Africa, village stores are owned today by men whose great-grandfathers traded in ivory and whose stores have served as ivory collection depots for over a hundred years.

Wherever elephants are at all numerous, they still represent the major source of easily accessible wealth and they are seen as a focus and a challenge for the energies of young men. Legal or not, hunting elephants remains a tradition that is important for more than purely economic reasons and there are still routes from the villages out to the world's major ivory markets.

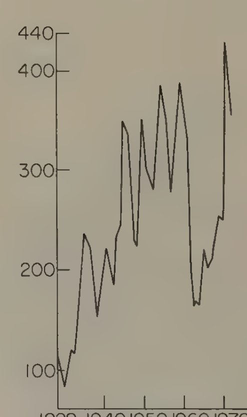
From the earliest times, administrations have attempted to earn revenue from this major source of wealth, but because ivory is easily hidden or disguised only a fraction of the trade has passed through official agencies, where licences are issued and weights are measured. For example, official sources in Kenya recorded a total of 370,000 elephant deaths between 1931 and 1969. On the basis of what is known about elephant population dynamics, Watson *et al.* (1972) estimated that this represented 19% of total mortality. As over 50% of all deaths are of tusked animals much less than half the total ivory production enters into official records.

Of course many elephants die where their tusks are never found but a small measure of unofficial trade can be found in recent import figures from one of the major ivory markets.



Imports of Ivory - Hong Kong (approx 70% of this ivory is estimated to come from East Africa)

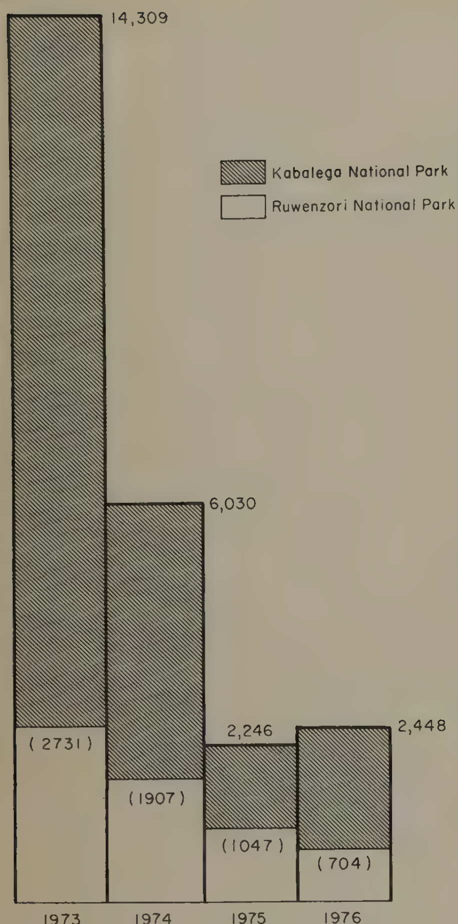
Hong Kong buys 47% of East Africa's ivory and 60% of its ivory supply comes directly from East Africa but because it is an open trade and there is little incentive to smuggle ivory in, the import figures provide a revealing comparison with the official exports from East African countries. For example, between 1971 and 1973 Uganda official records show exports to Hong Kong totalling 32·6 tons. In contrast, Hong Kong's records of ivory imports from Uganda for this period were 166·5 tons. In the 1970s there was a steep rise in the world price of ivory and political changes in East Africa led to ivory becoming a vehicle for the flight of capital, which pushed the black market price up from \$50 a kilo to over \$700 a kilo. The ivory rush gained momentum and by 1973 about 1,000 elephants a month were being killed in Kenya (Moss, 1976).



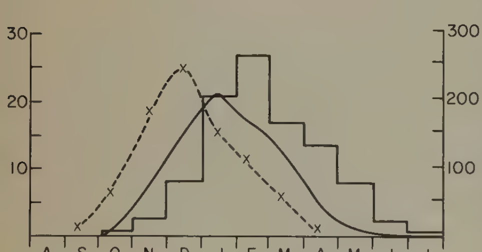
Official ivory exports from East Africa - 1929 - 1973

The Kenya Government's ban on hunting and trophy dealing has undoubtedly curbed poaching and the principal focus for large-scale ivory poaching is now Zaire and the Central African Empire. In Zaire official exports in 1976 were less than 1·5 tons but import figures for Hong Kong, Belgium and Japan indicated real exports of about 400 tons of ivory, representing the death of some 50,000 elephants. About 200 tons of ivory left Uganda in 1976, (Hammond 1977).

The great die-off of elephants in Tsavo during 1971 (a concentration which was itself influenced by intensive hunting pressure outside the park) showed a leap in Kenya's official ivory exports, which rose in one year from 50 tons to 270 tons. The overall rush into ivory was reflected in Hong Kong's ivory imports as rising from 270 to 600 tons.



Decline of elephants in two of Uganda's National Parks. (If average weight of ivory per elephant was 10 kg this represents a loss of over 960,000,000 Ugandan shillings to Uganda at the prices current at the time.) (Data from K. Ettringham and R. Malpas.)



Histogram of estimated conceptions for Luangwa elephant population with mean monthly rainfall (solid lines and given in mm on right axis and extrapolated birth peak (x---x---x and left axis). (Based on Hanks, 1969a.)

Large numbers of elephants cannot be killed today without the knowledge of government officials and there is a high risk of detection in large quantities of ivory being moved about. In 1973 Kenya newspapers reported 153 unlicenced tusks in the possession of D. Wambui, 32 tusks with K. Thiongo and a lorry was caught by the police in Witu with 300 tusks. In 1974 more than 800 tusks were turned up in a police raid in Nairobi (Lewin, 1975). In these and several other instances the cases were withdrawn and no prosecutions were made. The government invited corruption in 1970 by a highly significant change in policy. This was to allow the Game Department to sell ivory privately to individuals at unspecified prices. As a direct result of this the government's public auction rooms in Mombasa closed down for a time because "in the end only a small proportion of the material was changing hands in genuine deals; much of the rest is known to have been bought by civil servants and officials of all ranks at what are reported to be give away prices" (Lewin, 1975). In such situations the civil servant in charge of ivory transactions is subject to two pressures. On the one hand a favourable price to the buyer may be sought by bribery or, if this fails and the buyer has political clout, instructions may be obtained from a more senior level.

Of course, once such a channel exists for trade in wild-life products, other trophies become involved and there was a celebrated case in 1973 in which permits for 26,000 *Colobus abyssinicus* skins were issued to one person as well as for very many thousands of zebra hides. These details are given to illustrate that elephants and wildlife in general are threatened much less by the legitimate economic progress of the people than by international markets exploiting unsound national policies and at a local level by dishonest politicians and greedy people in influential positions.

Elephants can breed throughout the year but in several areas there is a very pronounced birth peak just before the height of the rains (see diagram). This timing allows a baby elephant to spend its first months in cool conditions surrounded by abundant cover and wet-season calves are better able to cope with drought by the time they are six or seven months old. By contrast, dry-season calves may have to walk long distances, exposed to heat and predators or else stay in the vicinity of waterholes, where the lack of forage soon hits the mother. In either event, both parent and offspring lose condition fast and there is evidence that mortality rates are higher for calves born during the dry season and also for those born in localities where physical conditions are generally poorer. This has been shown to be true for the North Bunyoro elephants, which have an impoverished habitat and no tree cover to provide browse or shelter in the dry season. This artificially compressed population has been compared with an adjacent population to the north of the Nile, where the elephants live at nearly half the density on an identical climate but in a habitat that still has some woody tree cover. Sexual activity, betrayed by the number of conceptions, goes on throughout the year but the North Bunyoro population is less prolific and has a conception peak five or six months later than their neighbours to the north, a delay that results in a dry-season birth peak with greater mortality of calves.

The gestation period is 21—22 months so that mating peaks take place two or three months after birth peaks. Few cows come into oestrus before their calves are two years old and there are considerable individual and

regional differences in the calving interval, ranging from two-and-a-half to nine years. When a high proportion of calves are dying this would speed up the average intervals between births as anoestrus is linked with lactation. However, this effect could be somewhat masked if communal suckling takes place.

Perry (1953) suggested that oestrus may recur at about two-month intervals but, once she has come into season, a female is unlikely to be missed by the bulls, which make very frequent visits to the family units, each time sampling urine and faeces with the tips of their trunks and circulating among the females feeling their genitalia. It is known, however, that some females have ovular cycles without conceiving. Although the mechanism suppressing fertility is not understood it may be influenced by the need for an accumulation of corpora lutea (see below), nor is it known whether males can detect these sterile oestrus-cycles. The problem is an interesting one in the context of the elephant's social organization, for the suppression of breeding in inferior females is known in other highly matriarchal societies such as *Helogale* and *Mungos* (see Volume IIIA, pp. 196, 223).

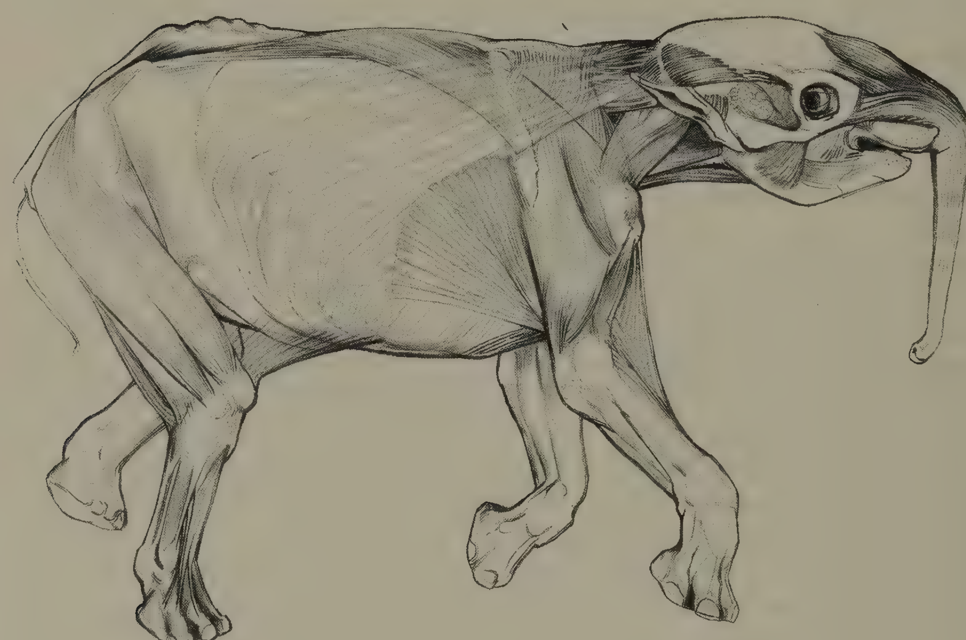
When first approached by a courting bull the cow may retreat, manifesting her fear with rolled-up trunk, or else she may be provoked into a mild pushing contest or head-on confrontations. The male repeatedly lays his trunk over her back. Deliberate embracing or grasping by the male's trunk may have an intimidating effect but it certainly appears to check her movement. Male behaviour in the presence of an oestrous female is very variable and sometimes there is intense competition and fighting. As many as ten bulls may follow a single cow, giving vent to their interest with much growling or even trumpeting, their colossal curved penises wagging about in grotesque and dribbling disarray. At other times there are no signs of competition and discreet and silent copulations take place with the minimal disruption of other activities and few preliminaries. An elephant's oestrus probably lasts only a day or two and observed differences in the intensity of male interest may be related to the timing of her peak.

Sometimes the cow solicits attention by backing into a bull or by rubbing her peniform clitoris against him; this may be followed by a run although it is quickly halted by the touch of the male's trunk; in the course of these chases, males have been seen to take the female's tail in their mouth and butt her hindquarters. Before taking the male's weight on her back the female widens the stance of her hindlegs and leans back but sometimes she may be sufficiently uninterested to continue feeding. She may be mated in succession by one or several bulls to the accompaniment of growls, trumpets or silence, the copulation lasts from half to one-and-a-half minutes.

The mechanism by which the embryo is retained within the uterus for nearly two years was one of the problems that invited an investigation of the elephant's reproductive physiology by Perry (1953). He originally suggested that pregnancy was maintained and replenished with the development of secondary *corpora lutea* during mid-pregnancy but Buss and Smith (1966) have shown that *corpora lutea* last for the entire pregnancy and can still be present when the elephant returns into oestrus. Hanks (1971) has pointed out that *corpora lutea* seem to be necessary for the development of endometrial glands and a critical mass of *corpora lutea*, accumulated from suc-

cessive oestrus-cycles, must be achieved before conception can occur. Large *corpora lutea* are common in pregnant animals and their life is prolonged by the presence of the embryo. Hanks could not detect progesterone in the peripheral blood during gestation and the *corpora lutea* secrete so little that the pregnant elephant either finds the hormone unnecessary or is extraordinarily sensitive to it.

Abortions occur and Laws and Parker (1968) dissected out necrotic foetuses in cropped elephants. An elephant in Samburu died as the result of aborting an incompletely-formed foetus and there are also reports of females dying after giving birth to full term calves.

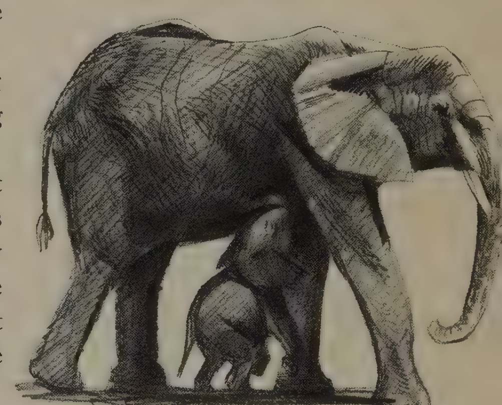


Females have been recorded giving birth on their own or within a family group, in cover or out in the open, and the strength of the newborn baby seems to be very variable, some rising on to their feet almost at once, others not walking for an hour or more. When the other members of the family are present, they may form a defensive circle if disturbed and excited or they may continue to forage, but there is usually much competition to touch the baby and nudge it to its feet. However these impulses can scarcely be differentiated from those that bring members of the family to the aid of any fellow in distress, whether it is a youngster bogged in a wallow or an adult felled by a bullet. Hamilton reported a family group occasionally stopping and moving at an unusually slow pace when there was a new baby but the natural onwards movement of the unit may sometimes leave a mother alone with her new offspring. Isolated mothers in such a situation have been seen to break and toss branches and other vegetation, which is the typical displacement

activity for elephants. Tension is probably generated by the mother's desire to keep with her family and the need to stay with her still immobile calf and the discovery of trampled bough-strewn arenas made by new mothers have given rise to the widespread belief that elephants build themselves "bomas" to give birth in.

An hour or so after birth the placenta is dropped and a mother has been recorded attempting to eat a portion. A new baby may need some help in standing and walking and the mother or other members of the unit may support it with their trunks. Within three days progress is generally normal but some shakiness of the legs can sometimes be detected during the first month; thereafter the baby has little difficulty in keeping up with the family. Hamilton noticed that the younger mothers are the most maternal and these cows may be the most ready to suckle other calves or adopt orphans. The older cows are less tolerant and maternal behaviour is not always exemplary. Stephenson (personal communication) saw a female trample her two-week-old calf to death and a bemired baby that was rescued by a warden at Maralal was tusked to death when it rejoined its family, possibly because of the human scent it may have acquired.

While still very young, the baby keeps contact with the mother by leaning heavily against her legs and this infantile trait may be the origin of the leaning behaviour of adults in their defensive formations.



The mother keeps a very close watch over her young one during the first six months of its life and continues to be aware of its movements until it is over a year old, a very necessary attention since the baby is completely fearless at first and very exploratory (lions have been seen waiting for the opportunity to seize such a straying calf). The young seek one another out and engage in much challenging, wrestling and mutual pushing when the family is resting or drinking.

Weaning is normally drawn out from about six to eighteen months but milk is sometimes drunk by elephants that are six years old or more. The mother's tolerance of sucking varies and it may be strongly influenced by the growth rate of the youngster's tusks. These grow at quite different rates in different individuals, so that some quite small animals may have relatively long ones while a very large elephant may have stubby tusks. The readiness of other elephants to care for young ones is apparently not always restricted to females and Rushby (1953) saw a nine-month-old calf which was in the company of some bulls attempting to feed on the bark that they were stripping.

The age at which a young elephant reaches puberty is probably determined by nutrition but may possibly be influenced by social factors. The variation of this age between eight and twenty years in males and ten and twenty-two in females (Laws and Parker, 1968) will obviously alter the dynamics of population growth quite fundamentally. Likewise, poor nutrition might generate infertility and thus a female's reproductive life may be shortened at both ends. However, Hanks (1972b) on the basis of mathematical population models regarded increased birth intervals as having the most significant influence on population dynamics. Whether due to natal mortality or reduced fertility, birth frequencies respond directly to the vicissitudes of the environment.

Any single population is constrained by the climate through its need for adequate food, drink and perhaps shelter from the sun. These in turn can be affected by the relative density of elephants if they use up the resources and destroy shade. It is known that high densities can be sustained in rich habitats without obvious stress, but the removal of all tree cover generally means that elephants are subject to malnutrition and probably heat stress during the dry season with the young and adult females dying in the greatest numbers during years of drought. Nearly 6,000 elephants died in Tsavo during the dry years of 1970—71.

They died in areas of the park where there is permanent water but where rainfall is low and unreliable. Here immigration and concentration of elephants has led to the destruction of thicket and bush on such a large scale that the animals died of starvation. That the numbers of elephants in South-eastern Kenya had been increasing since about 1957 (by which time elephant hunting was effectively controlled and limited by Government agencies) has been deduced from studies of the age structure in Tsavo (Laws, 1970b). Since then agricultural expansion has reached the boundaries of the park from several directions while water supplies outside the park are increasingly monopolized by pastoralists. Drought served to concentrate the animals still further while uncontrolled poaching reached such proportions in 1973 that Moss (1976) estimated 1,000 a month were being shot in Kenya. The situation was the product of two opposite pressures which are operative for most elephant populations today. One is the natural growth of numbers through breeding, the other is a general compression of the elephant's range through the rapid expansion of human population and settlement.

Although greatly accelerated in recent years, this expansion of the human population has been continuous over the last thirty years and over this period more than half a million elephants have been shot in East Africa. Most of the shooting has been along the frontiers of agricultural expansion. Crop protection and the supervision of government interest in the ivory trade was the principal *raison d'être* of the Elephant Control Units which later became the Game Departments. In spite of dispatching many thousands of large and valuable animals, the colonial departments kept no records beyond ivory weights and receipts. Contemporary biologists trying to study an animal with a life-span of 60 years have justifiably reproached the Game Departments for neglecting to record data. Criticisms were voiced in the 1930s; yet it was only in the 1960s that the policies of these departments became accessible and receptive to independent scientific counsel.

The need for retrospective data became acute when Laws and Parker started their studies of population dynamics, which revealed that the control operations had had a profound effect in North Bunyoro, where over a quarter of the elephants had been shot in the course of twenty years. Comparisons of this highly compressed population with those in other regions revealed a totally different age-structure as well as other peculiarities which have been mentioned earlier. For example, it was estimated that the mortality of calves may have been in the region of 20% in 1953 and 38% in 1965. Summaries on the various regional studies of elephant population dynamics are available in Laws *et al.* (1975), Hamilton (1972) and Croze (1974).

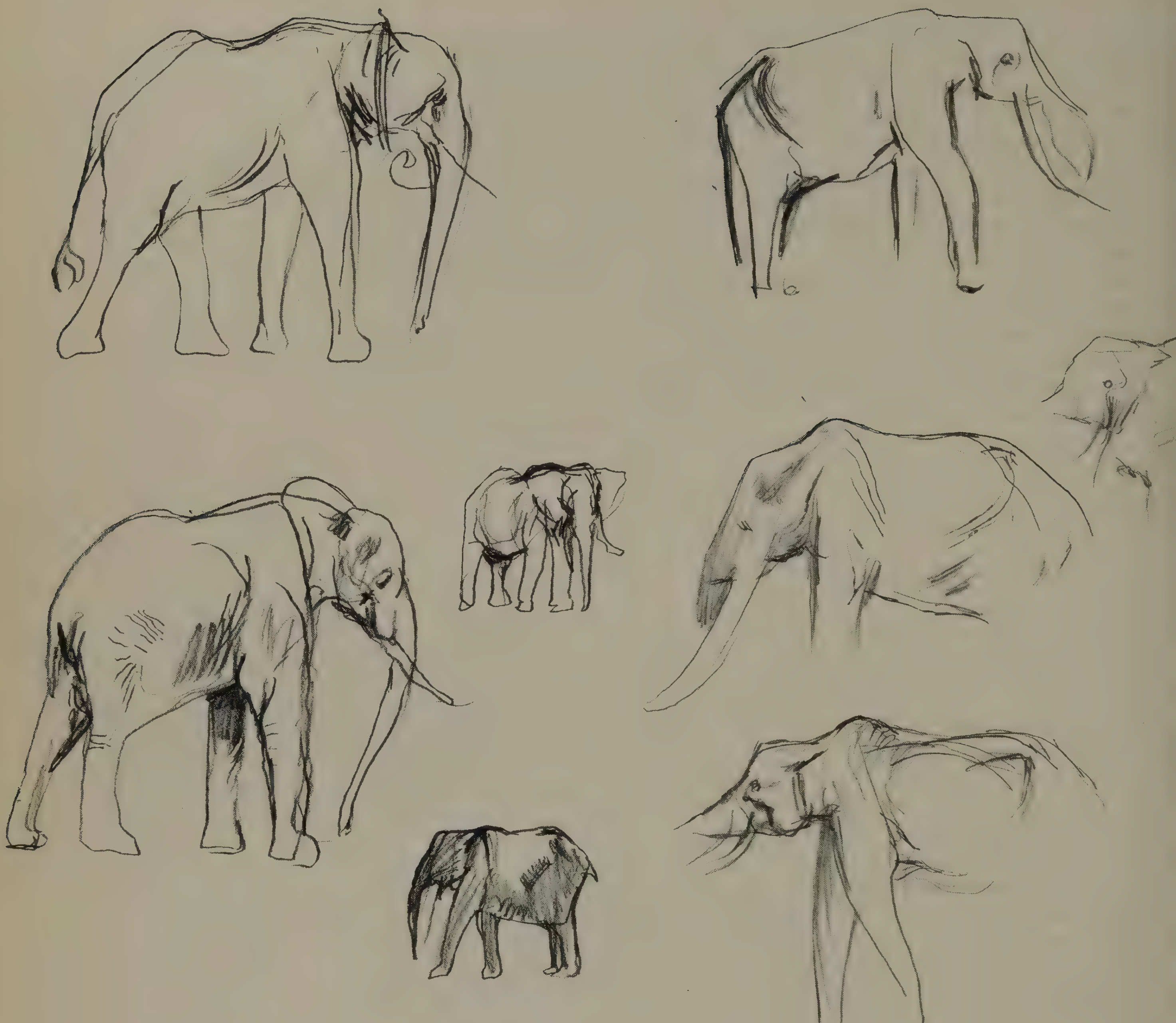
Recent studies on the biology of the elephant have shown that a rational

and humane management of this animal is possible. They have also shown that the elephant is a major influence on the habitat and indeed must be managed once populations have become artificially confined, as so many are now; and it has been proved in Uganda and in northern Tanzania that rational cropping programmes can finance themselves from the meat and ivory, at the same time providing a great deal of valuable scientific data. They have also narrowed the line between managing domestic and wild animals by producing an inventory of the stock, with breakdowns by age and sex, by calculating energy flow at different stocking rates and by predicting the effects of numbers on the habitat and on other species of ungulates. But perhaps most important of all, we now realize that we are unlikely to achieve a proper understanding of any of the major ecosystems of tropical Africa if the elephant is left out of account. A great deal remains which can only be discovered after many years of systematic measurements and study.

In 1973 the Kenya Game Department estimated that there were over 167,000 elephants in Kenya. In 1977 the Elephant Survey and IUCN Conservation Programme indicated a loss of nearly 100,000 elephants in four years and that the total population stood at about 70,000 in 1977. A detailed breakdown of numbers in Kenya's rangelands confirm the drastic decline. The map indicates estimated numbers in Kenya rangelands in 1977. From Ministry of Tourism and Wildlife Aerial Survey No. 3.

The best interests of the local people and their governments, of science and of conservation will be served by elephants being managed and controlled under definite national policies that continually monitor their own programmes and are adjustable in accordance with the information that accumulates. Accurate records of kills must be kept and the agencies responsible for management should be receptive to scientific counsel at all levels and their operations must be open to independent scrutiny.

That large numbers of elephants are incompatible with forestry and agriculture is unquestionable; that they are too numerous in some areas is proven; and that they will become a worse problem in the future can be predicted unless the situation is overtaken by events. This has shown signs of happening; the culling that was recommended by ecologists during the sixties has been partially achieved by the starvation of 6,000 elephants in Tsavo during 1970—71 and by a hunters' ivory rush since that time when the price of this commodity rose. The boost of ivory rose out of long-term speculation of investors during a period of economic instability. These speculators realized that elephants will become scarcer and that ultimately ivory would become a non-renewable commodity, which would enhance its rarity value.



This would eliminate its currency value, which would deprive East Africa of a very valuable natural resource. This assumption is based upon the present trends of human population growth and on an established pattern of elephant exploitation which has generally treated them as a wild resource to be plundered while it lasts. These events suggest that environmental and economic forces will eventually dispose of the problems posed by elephant numbers in a brutal and wasteful way. The people and economies of East African countries, science and all who care for the welfare of elephants will be the losers if there is no recognition of the need for international elephant

policies. Such policies can only expect to be of general benefit while the animals are sufficiently numerous to be a problem, sufficiently numerous to make a contribution to the economy and sufficiently numerous to support an ambitious biological programme. Furthermore, we still have the opportunity of learning about the impact of great numbers of highly social and successful animals in a wide variety of habitats.

The ecological impact of this, the largest land mammal, on its environment is on a scale that cannot be matched, simulated or reconstructed and a special value of elephant studies lies in the insight they provide into the past and into the most fundamental processes of ecology. We are only now beginning to treat the elephant with the respect it deserves; together with rain, sun, fire and man the elephant has been one of the forces that has shaped the ecology of Africa.

Since this profile was written the Kenya Government has commissioned an ambitious study of very large herbivores on which the nation's long-term policies are to be based. An inventory of the present stock and biologically informed management plans for the future are called for. The project also seeks accountability by considering the means by which administrative decisions may become matters of public record.

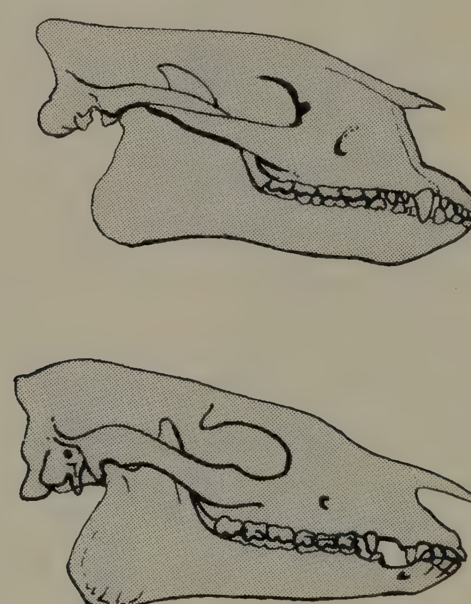
Even while two industrial superpowers plunder the world's diminishing stocks of whales it is encouraging that a small developing nation should pioneer the scientific conservation and responsible exploitation of terrestrial large mammals.

Perissodactyls

Perissodactyla
Equidae
Rhinocerotidae

Perissodactyls must have emerged from a primitive ungulate group, probably during the later Palaeocene, a period that is poorly represented in the fossil record. Their most likely ancestors are condylarths, some of which were probably omnivorous but had the general mien of carnivores or insectivores, with a full dentition, differentiated canines and a relatively long skull.

Although it is too large and too late to be considered directly ancestral, *Phenacodus* (see Volume I, p. 376) is intermediate in the structure of its heavily nailed feet and in some features of its skull and dentition between a generalized early mammal and the primitive Eocene *Hyracotherium*.

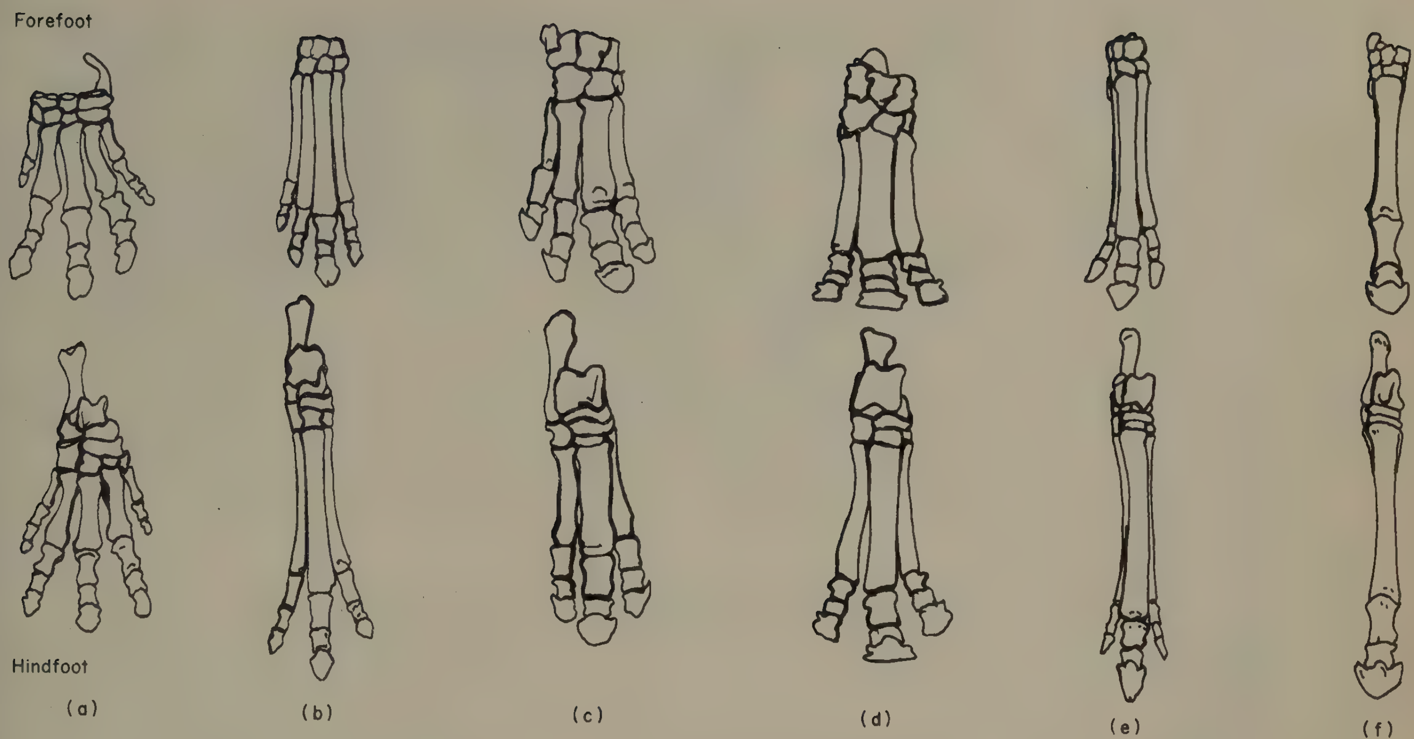


Skulls of Eocene condylarth, *Phenacodus primaevus* and *Hyracotherium* compared.

Hyracotherium is the earliest perissodactyl and may be close to the common ancestor of horses, rhinoceroses and tapirs although its slender proportions already anticipate those of the equids. Its niche may have been close to that of the living tragulids.

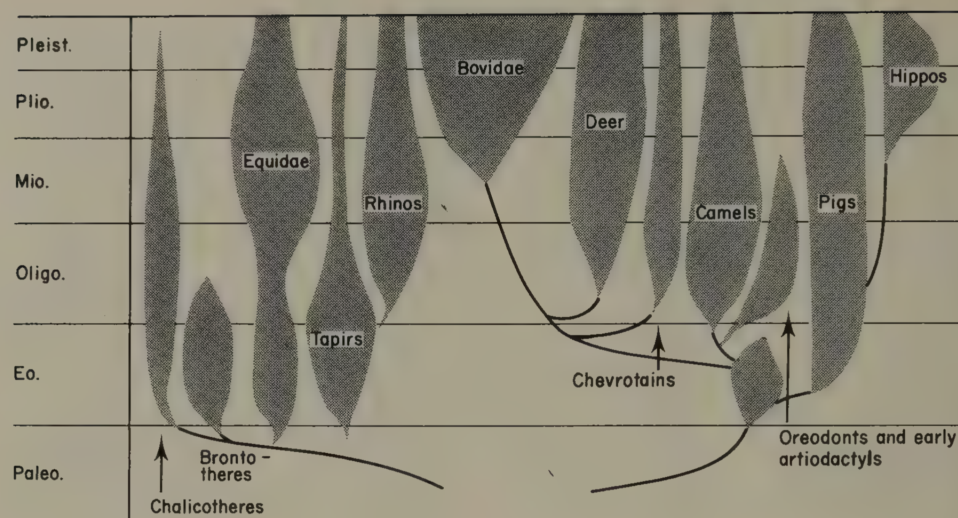
Later, perissodactyls tended to be large and to carry their weight on three toes and in modern equines on only one toe, hence the clumsy anglicization "Odd-toed hoofed mammals".

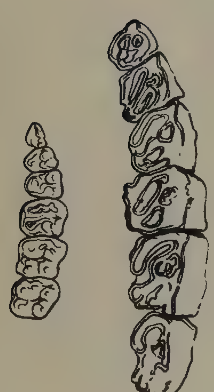
Perissodactyls diversified in the Eocene and were among the most abundant of herbivore types in America and Eurasia up to the Miocene.



Above: Perissodactyl lower limbs: forefoot above, hindfoot below.
(a) *Phenacodus* (Condylarth);
(b) *Hyracotherium* (primitive perissodactyl);
(c) *Tapirus* (Tapir);
(d) *Diceratherium* (Miocene rhinoceros);
(e) *Miohippus* (Miocene horse);
(f) *Equus*

Left: forefoot, black rhino.





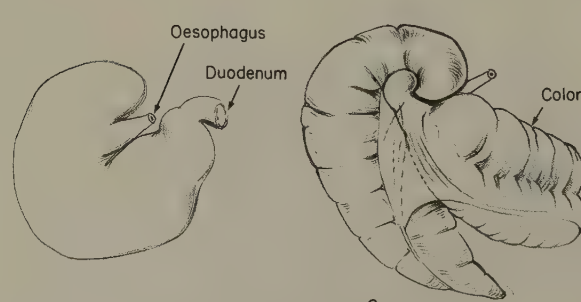
Left: *Hyracotherium* Right: *Ceratotherium*.

Superior digestive assimilation by advanced artiodactyls probably led to competition and the progressive elimination of perissodactyls from all the ordinary herbivore niches but the survivors appear to have become specialists in coarse feeding, or in the case of the grass rhino, *Ceratotherium*, an advantage may have been gained through gigantism. Browsing rhinos can feed on woody vegetation too tough for the bovids' leaf-plucking mouth and the horses have the advantage that their teeth can manage the wiriest grasses, while *Equus* may have acquired some competitively superior adaptations in their social life (see p. 128).

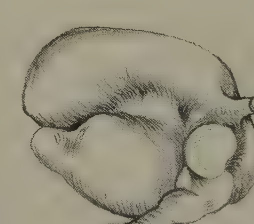
In Africa, perissodactyls have always occupied special niches and arrived too late ever to have been a dominant group (see Volume I, pp. 55—58).

The relatively late adaptation in Africa of *Ceratotherium* to a grass diet is interesting, suggesting that large size may confer a high level of immunity from predation and reduce the impact of competition in rich well-watered habitats.

It has been calculated that the ruminant type of digestion is advantageous up to a body weight of 1·800 kg (Van Soest in Janis, 1976). Janis (1976) regarded large size in rhinos as a strategy to avoid ruminant competition and



Stomach and caecum of *Equus*



Complex chambered stomach of an advanced ungulate

suggested that the rhinos might be regarded as representing a real adaptive response of the Tapiroidea to changing evolutionary pressures at the end of the Eocene.

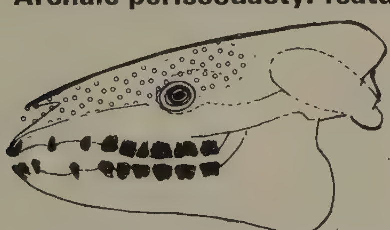
Turning to the origins of perissodactyls as herbivores, Janis (1976) thought they adopted a diet containing cellulose during the Palaeocene while they were still relatively small. She pointed out that all small-sized herbivores that eat a lot of coarse vegetable matter, lagomorphs, hyraxes and some rodents have developed caecal fermentation and she considered that the body size of ancestral perissodactyls was the critical factor in determining the type of digestion.

If quantities of herbage are always available the perissodactyl system is actually superior to rumination at digesting a high fibre content. There are no advantages in rumination for a very small animal and Van Soest (in Janis, 1976) regards 5 kg as the minimal body weight at which rumination would be viable. It is known that ruminants developed very much later than perissodactyls (see table) and it is likely that artiodactyls adopted a truly herbivorous diet when they were already relatively large.

Only two of the three living families have ever been represented in Africa and it is possible that the tapirs never entered Africa because their niche was pre-occupied by early proboscids.

FEATURES INFLUENCING FORM IN PERISSODACTYLS

Archaic perissodactyl features



Vegetarian diet; rel. high crowned molars, deep jaws. Increasing size trend. Well developed olfaction in extended cylindrical skull.

Equid features

Medium-large size. Elongation of neck, legs and skull. Vision well developed; high head carriage. Diastema, molars with very high crowns with deep rooting. Incisors cut and pull grass. *Defence:* speed. *Weapons:* teeth and hooves.

Rhinocerotid features

Great size and weight. Heavy head, low carriage. Short plantigrade limbs. Vision poor; olfaction good. Incisors and diastema lost, lips gather food. *Defence:* size and horns. *Weapons:* nasal horns.

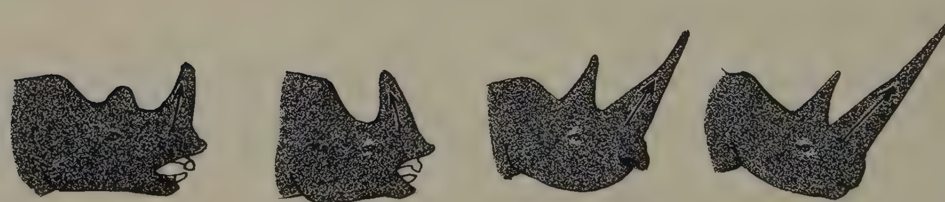
Ceratomorphs

Ceratomorpha
Rhinocerotidae

Genera

Diceros
Ceratotherium

When animals have become as scarce as the rhinoceroses are today it is difficult to describe them as successful without tedious qualification. Yet there is good reason to regard the living African rhinos as advanced and successful representatives of a family that has seen a very wide range of species and types in the past.



Dicerorhinus *Rhinoceros* *Diceros* *Ceratotherium*

Their name describes that unique peculiarity, the nasal horns: a characteristic that is probably as highly developed in the living species as it has ever been in any of their ancestral forms. It is interesting to note that there is a gradient in the size of horns in different rhino species. *Ceratotherium*, living a semi-social life in the most exposed habitats, has the longest horns while the Oriental rhinos, living a more solitary existence in dense jungle, have the shortest. It is possible that long horns get more in the way in a dense habitat but their employment in intra- and extraspecific defence is probably more developed in the former species. Furthermore there are phylogenetic implications; the short-horned oriental *Dicerorhinus* is a genus known from the Oligocene, whereas *Ceratotherium* only evolved in the Pliocene and is undoubtedly much more advanced.

From a photograph by F. Hartmann (1970).

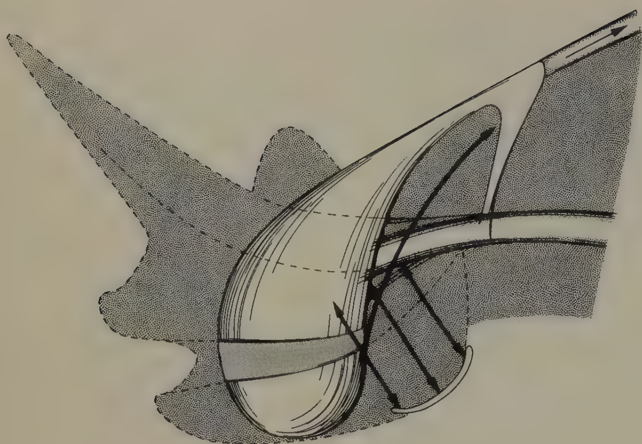
In the long-horned African rhinoceroses, horns tend to be used more as clubs than rapiers, particularly in the early stages of a fight. These sideways swipes, which occasionally cause horns to split, probably have a phylogenetic origin in defensive movements that deflected direct thrusts of the horns but have become ritualized into an effective and relatively harmless way of testing strength and may even be accompanied by shoulder pushing without horn stabbing (p. 115). A major conflict is of relatively rare occurrence because a dominant rhino is recognized by his scent and behaviour and elicits

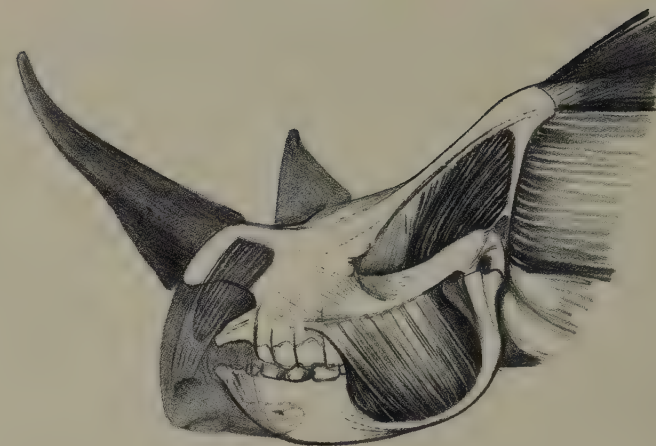
submission or avoidance in all other rhinos living in his territory. The richer the resources and the more open the environment the more frequent are contacts likely to be. It is therefore possible that ritualization has proceeded further in the African species than in the short-horned, forest-dwelling rhinos of Asia. It would be interesting to compare the details of horn fights or clashes in the more primitive *Dicerorhinus* and *Rhinoceros* with those of the African genera. The imminent extinction of *Dicerorhinus* makes the possibility of such comparisons sadly remote. Females are well able to defend themselves but they seldom fight. A mother protecting her offspring during a capture campaign has been seen to toss a 450 kg horse high into the air easily, which illustrates the strength of rhinos and emphasizes how dangerous all-out fighting with horns can be.

Very occasionally a rhino is born without horns. Conversely, the rudiments of a third or fourth horn may sometimes appear either behind the others or on other parts of the body. The famous engraving of an Indian rhino by Dürer shows just such a supplementary horn on its nape; however this picture was a copy from a Portuguese artist's work and the spike might have been an artistic elaboration. Areas of reinforced and rugose bone on fossils suggest that there was a general tendency towards clusters of knobs or horns on the head of various extinct rhinos.

Left: Great Indian rhinoceros, showing sites of small accessory horns above the eyes and on the forehead. Right: Black rhinoceros from a photograph by K. Sheldrick (1975).

The earliest and most primitive ancestral families, Hyrachidae and Hyracodontidae had no trace of horns and small "running rhinoceroses" were evidently fast and agile and would have resembled something between a tapir and a horse in appearance.





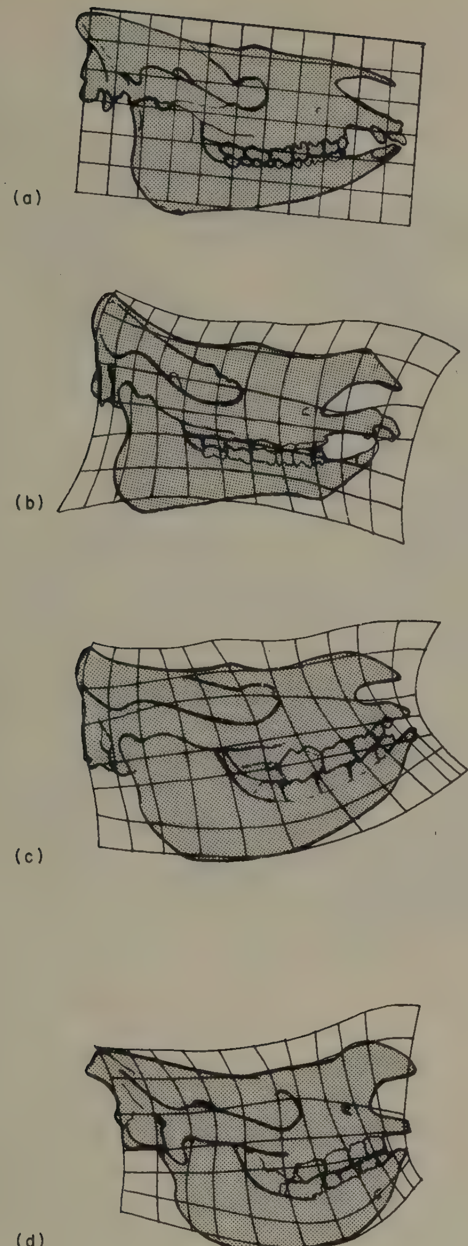
Ceratotherium: principal mass of skull in relation to mastication, horns, vertebral column and suspension.

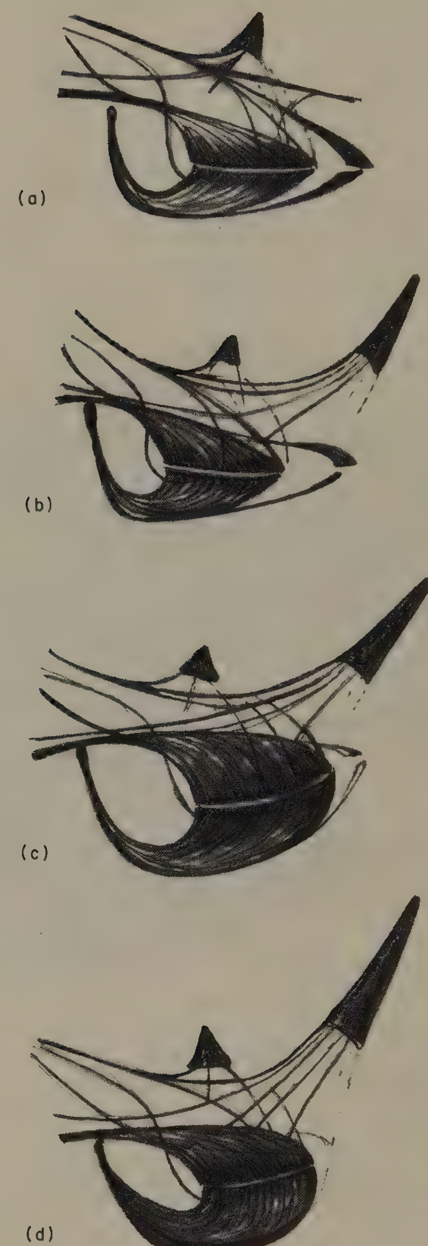
All the perissodactyls have retained their dependence on the sense of smell for information and intraspecific communication, but the rhinos live in a world in which scents are the prime regulators of their social existence. Both their rhinencephalon and olfactory chamber are exceptionally large (Friant, 1955). The latter is accommodated beneath the cantilevered nasal bones which have had to be well buttressed to take the stress of the keratinous horn (see drawing). The massive teeth have even stronger bony bases and reinforcement of the forehead and occipital area allows an adequate support for the weight of such a heavy head as well as providing a bony shield for the brain. Enclosing large cranial, olfactory and buccal cavities, articulated by huge jaw and neck muscles, reinforced against its own weight and the extension of its horns, a rhino skull is a splendidly architectural model of form and function.

Ancestral rhinos, such as *Trigonias* and *Caenopus* had a diastema, incisors, even canine teeth and the nearly extinct *Dicerorhinus* of South-East Asia has retained short tusks in the front of its mouth. The African rhinos, instead, have lost their incisors and there are now only bony vestiges in front of the cheek teeth which have made a phylogenetic migration forward to the front of the mouth and head while the lips alone do all the cropping or plucking of food. A habit that may derive from the time when they had incisors is the snarl; Oriental rhinos actually bite but the African species employ the snarling gesture when they are on the defensive and being threatened by a superior.

Dicerorhinus has been found in the Upper Oligocene in Asia and in Europe and Africa in the Miocene and members of this genus were once very widespread. The woolly rhinos of the ice ages, *Coelodonta*, were closely related to this genus.

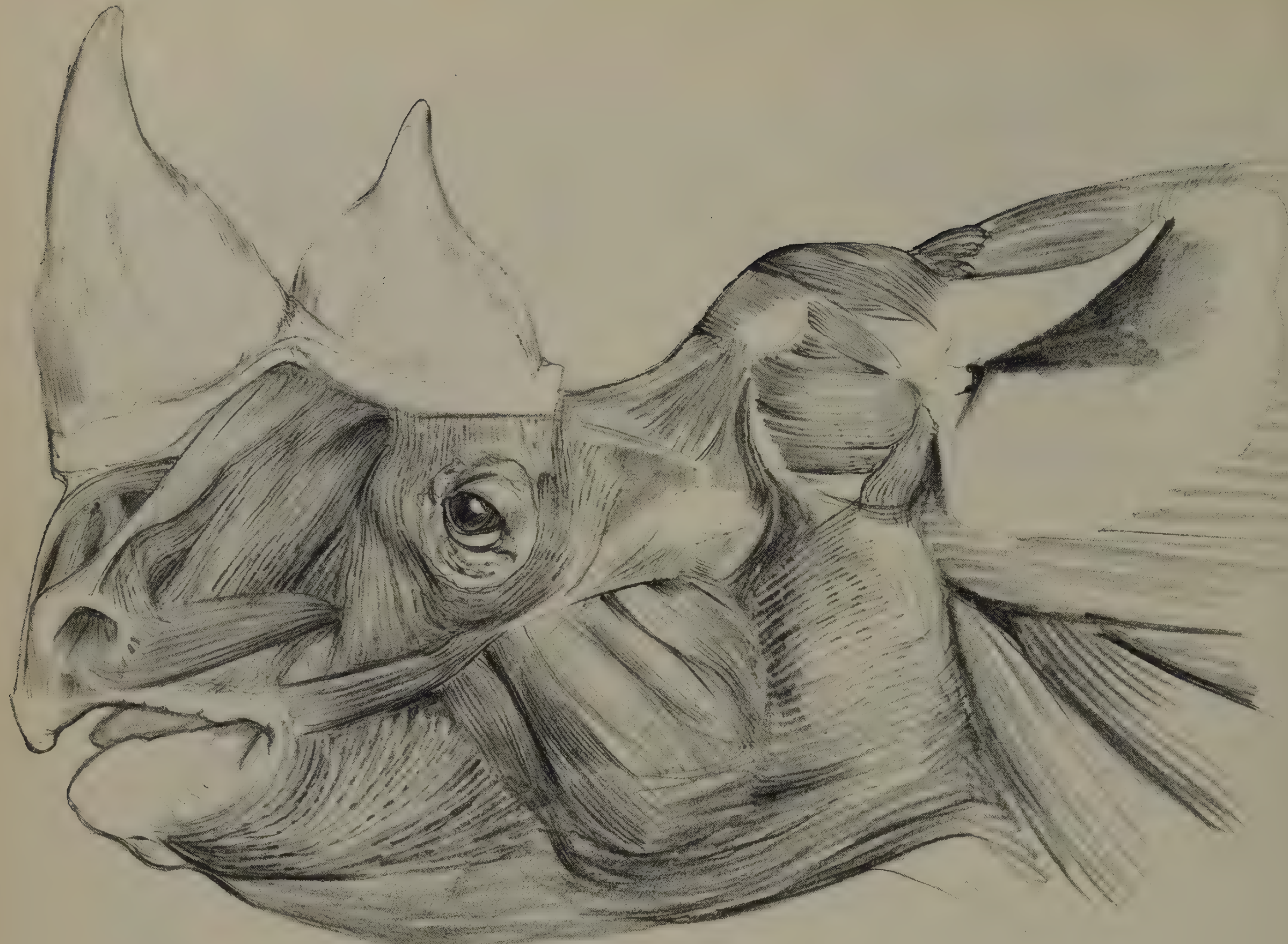
At least one rhinoceros species, *Paradiceros mukiri*, appears at Fort Ternan and this species may have been ancestral to both living species as well as to the extinct *Diceros pachygnathus* which occurred in Europe. Previous to this the hornless *Aceratherium* and *Brachypotherium* (belonging to separate and dead-end branches) appear in the East African Miocene.





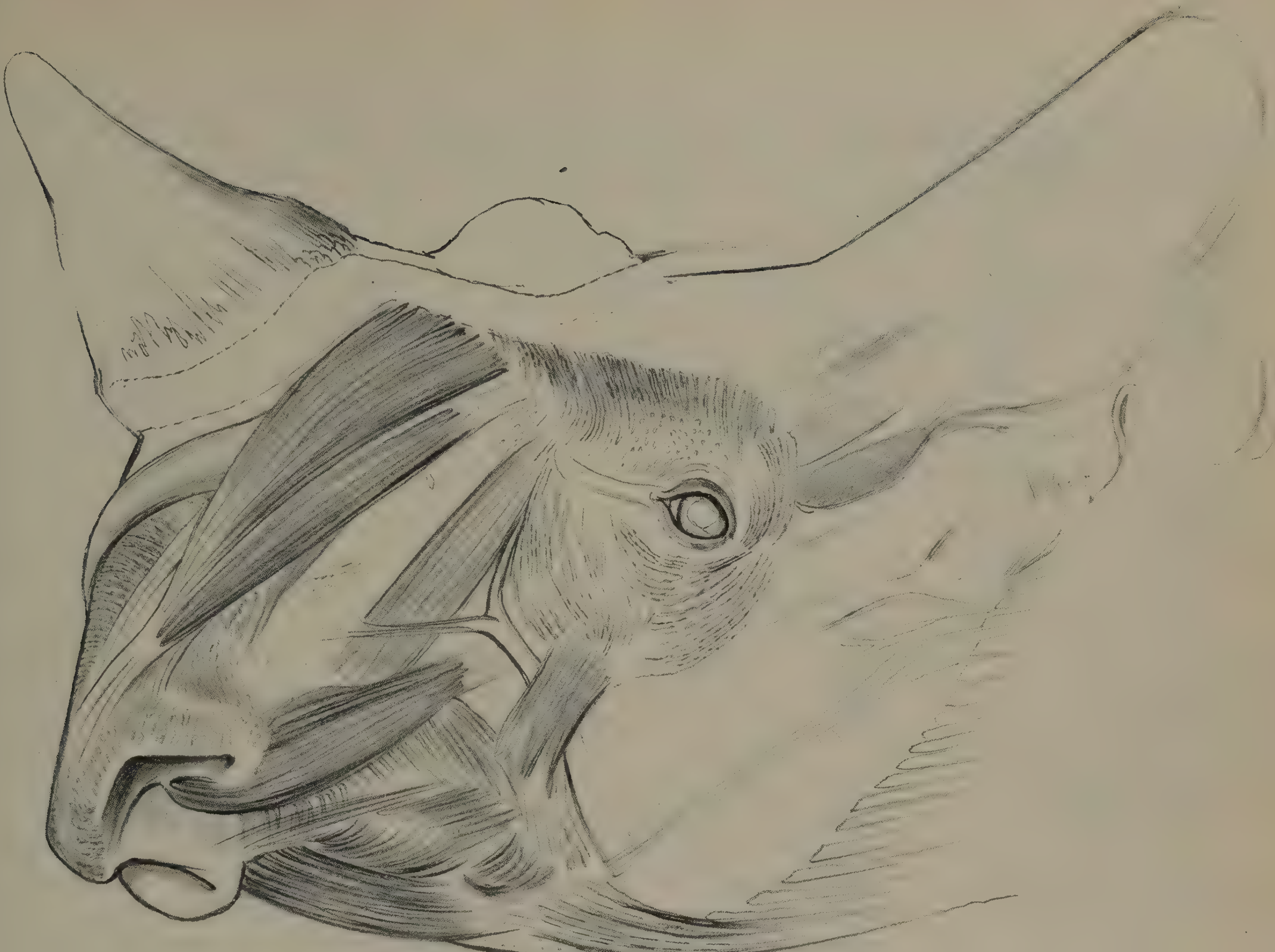
Buttressing of the skull in rhinoceroses in relation to teeth and horns.
(a) *Caenopus* (Oligocene);
(b) *Dicerorhinus* (Oligocene-Present);
(c) *Paradiceros mukiri* (Pliocene);
(d) *Ceratotherium* (Pleistocene-Present).

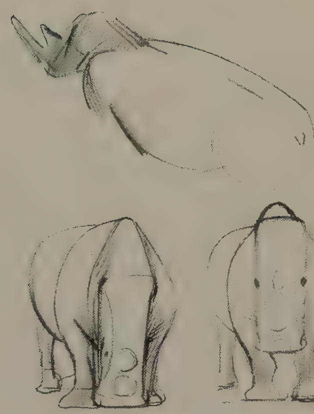
By the early Pleistocene both modern genera are present, *Diceros* in its present form while *Ceratotherium praecox* from Chemeron (4 million years old) still shows decided resemblances to *Diceros* but is probably directly ancestral to *C. simum* (Hooijer and Patterson, 1972). A Pliocene rhino from Samos, *Diceros pachygnathus*, has some characteristics of both genera and it has been suggested that they should be lumped in a single genus. Examining blood proteins, Osterhoff and Keep (1970) noted a great genetic variability in *Ceratotherium* while *Diceros* showed no variability whatever. Inferring from work on domestic animal breeding, they link this variability with an active stage of development, in which case the black rhino should be the more stabilized species. *Diceros* possesses 84 chromosomes while *Ceratotherium* has 82.

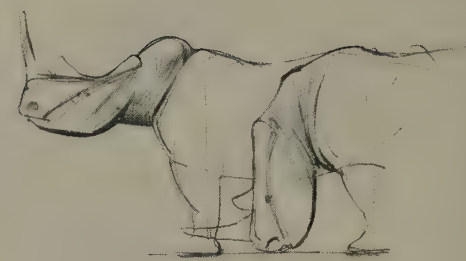


Above and below: *Diceros*;
Opposite: *Ceratotherium*.

By invading the open grassland, *Ceratotherium* has departed furthest from the ancestral rhino niche of browsing coarse vegetation in thick undergrowth. The implications of this change are readily manifested in a comparison between *Ceratotherium* and *Diceros*. The most commonly described difference between the two species is in the structure of the mouth. The upper lip of *Diceros* is a pointed prehensile organ capable of wrapping round twigs, leaves, fruit and grass and thorns and drawing them into the mouth where they can be chewed or snapped off by the premolars. *Ceratotherium*, on the other hand, has flat-fronted lips, a very broad mouth which is especially adapted to crop short or medium-length grass and more hypsodont teeth. The acquisition of grazing habits has had far-reaching effects on form. Like horses, the ancient, gracile rhinos had relatively long necks so that dropping the mouth down to ground level was no problem, but as the true rhinos developed towards their present proportions they followed the common trend of increasing size, as body and head became heavier, limbs and neck got shorter. Contrary to popular belief, rhinos are not slow ponderous beasts because the greater leverage and flexibility of a light long-limbed animal has been replaced by the greater thrust and power of their well muscled bodies







Thoracic vertebrae of *Ceratotherium*.

(Smith and Savage, 1955). A more compact form allows tighter control of balance when galloping so that the neck must be short and the trunk relatively rigid. Paradoxically the browsing *Diceros* has a longer neck than the grazing *Ceratotherium* which has instead lengthened the head to reach the ground. Most particularly the occipital crest of *Ceratotherium* is exceptionally high, this may be influenced by the height of the glenoid condyle but the greater depth behind the poll improves leverage from the neck musculature while the backward sweep of the occipital crest slightly shortens its extent. Nonetheless, when the head is in the grazing position, the angle between the back of the head and the thoracic spines is wide and shallow; at least three times as wide as when the head is raised in the galloping or alert position. To overcome the shallowness of the angle, the last cervical spine is exceptionally long and mobile and acts as a fan spoke extending the arc of the hypertrophied *ligamentum nuchae*. The blade-like thoracic vertebrae are also exceptionally tall and have a unique adaptation to improve their flexibility without loss of strength; each spine has a posterior slot along its length into which the forward edge of the next spine can insert. As this arrangement only occurs in the white rhino it is evidently adapted to the extraordinary amount of contraction involved in raising a long heavy head. The demand for both strength and flexibility in the area of greatest bending moments would be particularly great during the gallop, at which time the head may be carried quite high (see drawing).

While on the brink of extinction today, rhinoceroses were evidently very widespread in the past. Numerous fossil rhinos have been found scattered across Africa and Eurasia. The woolly rhinoceros was carved and painted by stone-age artists right across the Palaeartic zone and preserved remains have been excavated from the permafrost of Siberia and the bogs of Europe. Schaurte (1960) reviewed the cave paintings and other early representations of rhinos. Likewise images of African rhinos are found wherever there are wall-paintings by cave-dwelling hunters and grass rhinos appear in rock paintings in North-central Tanzania, in the rock engravings from numerous localities in the Sahara and in the Kalahari, all areas where they long ago ceased to exist.

Grass rhinos depicted in Kisese rock shelter near Kondoa, Tanzania.

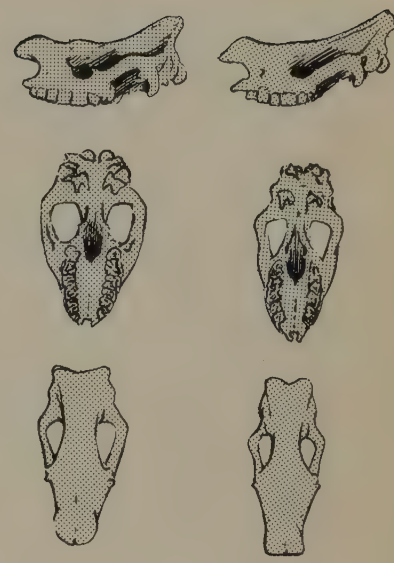
The ecological speciality of the rhinos was probably their capacity for

feeding on coarser plant material than most of the artiodactyls, yet with greater selectivity and less damage to the vegetation than elephants. Originally rhinos may have lived wherever there was a perennial supply of such food and water.

African rhinos depend on water for temperature control and they are capable of sweating to the point where their bodies are streaming with moisture. These scent-oriented animals have also a secondary use for water in their dependence on frequent sprays of urine for communication. Although it is only the sexually active minority that employ this device, the system would be less effective for a physiology designed to be economical of water.

Wallows are another necessity for rhinos and the wallowing habit probably assists temperature control, although it may have other incidental benefits.

Drought has been known to kill large numbers of rhino of both species. There was a massive mortality of *Diceros* in Tsavo in the drought of 1961. As conditions worsened in this area, rhinos from a wide catchment area concentrated around the only permanent water. Some months before the drought reached its peak there were reports of widespread and severe fighting among the rhinos. This phenomenon was possibly the product of the ecological disturbance shattering the established land-tenure network and is discussed later.



Diceros *Ceratotherium*

Thousands of elephants concentrated along the river and inflicted colossal damage on the surrounding bush. The forage for rhinos was thus reduced still further or actually destroyed. At the height of the drought rhinos were mainly dying of starvation but disease and stress were also playing a part. Elephants therefore appear to compete for browse with *Diceros* during periods of stress for both species. Whether grazing ungulates compete directly with *Ceratotherium* under similar conditions is not known, for relevant observations of the 1932 drought in Zululand are not available but Foster (1961) reported a decline in numbers at this time. However, there is a strong implication that both rhino species are susceptible to severe droughts and to the competition for reduced resources that attend them.

Large requirements of food and drink militate against rhinos during periods of extreme stress and their slow breeding inhibits a rapid recovery afterwards, so non-competitiveness with other herbivorous animals is most apparent over such periods and one can guess at similar factors leading to the decline of extinct rhino species.

The two modern genera are probably more adaptable and competitive than their collaterals and ancestors. Furthermore their recent decline is mainly due to man, but they also provide contemporary models for our understanding of the process of extinction.

Unaffected by rinderpest, they also appear to have a high level of resistance to anthrax, which is said to be endemic in African rhinos (Heppes, 1958). A low level of natural mortality has been noted in most rhino populations and this trait may be linked with their slow breeding rate.

Contemporary predators very rarely tackle an adult rhino and their imperviousness to predation is probably of long-standing. (Sabre-tooths might have been a major hazard in the Pleistocene but numbers of other pachydermatous mammals would also have been proportionally greater.)

Both species adapt their activity to the seasons, in that they rest for much longer in the middle of the day during the dry season. Otherwise their activity tends to alternate between feeding and resting throughout the day and night. Well-marked paths going to water or connecting feeding areas and wallows show that their habits are regular. These paths often pass through thick vegetation when it would be just as easy to skirt round it and the rhinos seem actively to seek the scratching sensation of twigs and thorns; they also like to rub on stumps and stones. In addition to the rewards of scratching an itch these habits may serve rhinos to help advertise their presence for the flakes of mud deposited or dropped off in this way possibly carry enough scent to be detectable to another rhino. If this is so, it is only one of several ways in which rhinos communicate with one another by scent. Apart from oestrous females only territorial male rhinos squirt urine and Owen-Smith (1974) showed that the frequency of squirting was highest in boundary areas between two *Ceratotherium* territories. He also considered this to be the main sign of territorial behaviour as a vanquished bull ceases squirting the moment he loses a contest. Urine probably identifies a rhino and his/her condition for other rhinos. Dung middens also serve as scent posts throughout the animals' home range, but Owen-Smith saw territorial bull *Ceratotherium* visiting particularly large middens on the borders of their territories where deep hollowing testified to the vigour with which the feet were scraped through them. He also saw non-territorial males use the same middens but with less ritual, as they may fail to wipe their feet in the dung or do it with less vigour and so probably make less smelly trails.

Scent trails provide the means by which both rhino species can meet or avoid conspecifics and encounters have been seen to be actively sought out by rhinos sniffing along trails. Non-territorial rhinos or territory holders off their own ground probably avoid other males, but there is evidence that resident males hasten to challenge invaders and that the distinctive urine ceremony is connected with territorial assertion. A male usually sprays urine over a landmark, a tussock, bush, stone or occasionally over a dung midden site, after which he lowers the head and thrashes his horn from side to side as if in the preliminaries to a challenge. This may be accompanied by backward shuffling or foot-scuffing and quick forward steps as if to challenge a non-existent rival. At times, the weaving of the head and horn turns into a savage onslaught on the bush or tussock. This horning behaviour has impressed many observers and has been widely interpreted as redirected aggression against an enemy. Owen-Smith's study established that *Ceratotherium* males have a well defined territorial system and although *Diceros* has been less intensively studied, there seems little doubt that the broad outlines of their social system are very similar. Only mature males are solitary and tend to restrict their movements even more than other classes. Both the density of rhinos and the food resources of the region are likely to influence the size of male territories.

Both these factors vary enormously. As many as 23 *Diceros*, of all sexes and ages, have been known to live in the 3 sq km of Lerai, Ngorongoro, 17 of them permanently. Even in the midst of inhospitable and extensive lava flows, *Diceros* can exist at surprisingly high densities and Root (personal communication) has seen 18 animals living in an area of about 15 sq km. Both species of rhino tend to crowd a suitable habitat rather than disperse out rapidly in

search of new ground. Five *Ceratotherium* per sq km of the Umfulozi Park has led to deterioration of the habitat and it is unlikely that densities of this order could be matched elsewhere; in the Kyle National Park, Condy (1973) found two *Ceratotherium* per 3 sq km and territories of 5—11 sq km. In Kidepo National Park, the overall density of black rhinos in 1970 was estimated at one per 10 sq km. The existence of male territories is obscured from casual observation by the tolerance of territory owners to other male rhinos (including former owners), so long as they show subordination in the dominant male's presence. Because the subordinate animal often displays noisy behaviour that gives every sign of being threatening, this has also tended to hide the true nature of confrontations between males, as has the behaviour of a territory owner the moment he steps outside the strict limits of his land. At such times, as on a trip to water, his movements become more tentative and should he meet any other rhinos, whether bull, cow or adolescent, while off his territory, he tends to avoid them. Owen-Smith (1974) has described some of the varied responses of other classes to a territorial male *Ceratotherium* on his own ground.

> "A subsidiary bull responds to an approach by a territorial bull by standing his ground, uttering loud rasping bellows with forward thrust head and flattened ears. He may even take a few quick paces towards the territorial bull. Despite their seemingly intimidatory nature, these gestures are to be interpreted as defensive threats. This snarl-threat is employed by cows and adolescents against an approach by a bull, and, among subadults, usually by the smaller animal. The territorial bull may approach simply to stare horn to horn, or may clash horns briefly. Such a horn clash is fended off by the subsidiary bull to the accompaniment of trumpeting shrieks. Engagements between a territorial bull and a subsidiary bull which is resident within his territory are usually very brief, and the territorial bull soon walks off, leaving the other bull standing. More often, however, the territorial bull simply wanders on past as if oblivious of the other bull's presence, despite nervous snorts and grunts from the latter. The two bulls may not infrequently be observed grazing or resting together peacefully only 20—30 m apart."

When there is a true contest for a territory the vanquished animal is seldom pursued far, nor is he normally attacked any further once he has fallen. There are scattered reports of extensive fighting among rhinos, which have usually been interpreted as competition by bulls in rut, but closer observation suggests that these outbreaks, which occur in both species, are mainly contests for territories by wandering males and are most likely to occur when the equilibrium of land tenure has been upset by ecological or other disturbances.

Unless they are in oestrus, females do not have their movements impeded by other rhinos and the extent of their range is determined by the resources of the area. These resources are shared by other females, subadults and non-territorial males. Females or subadults of both species wander over an average range of 10—12 sq km, with a wide range of variation. These classes, which are completely non-territorial and tolerant of other rhinos, are most frequently in twos. Most females accompany their latest young one and this association is the closest and most consistent bond in rhino society and is only broken just before the birth of a new calf. The rejected three- or four-year-old then forms a new bond, preferably with another youngster of the same

sex, or it may link up with an unattached female. Very occasionally the mother may tolerate its return some time after the birth of the new calf and, if the new baby is lost, the old association may be resumed. It has been suggested by Owen-Smith (1975) that the main social difference between *Diceros* and *Ceratotherium* is that the subadults of the latter are more gregarious.

When drinking sites become scarcer during the dry season, rhinos may walk greater distances away from their normal home range and especially attractive food or wallow sites may also draw numbers together into temporary congregations. The behaviour of such commuting rhinos is seldom indicative of their social status, as all classes tend to be equally diffident off their own ground.

Sexual behaviour would seem to be initiated entirely by the scent clues produced by the oestrous females. Courtship is cumbersome and exceptionally lengthy. The male on whose territory a female stands blocks her departure and, by attending her constantly appears to forge a temporary bond for the period of her oestrus, and very occasionally for a longer period. As she is invariably accompanied by her last young one or by some older female, the bull's advances involve a triangle. In the early stages of courtship, the cow and her satellite both repel his approaches and the bull may actually attack the cow's companion; she in turn may defend the victim and quite serious fighting can break out. The risk of conflict is evidently offset by the male being extraordinarily cautious but also persistent in his courtship. His capability for damaging the young or the female is probably countered to some extent by the fact that females are just as well armed and sometimes nearly as heavy as the males. The fact that subadult companionships may be between members of the opposite sexes as well as between bachelors, shows that the only period in which rhinos assume obvious sexual roles are when a female comes into oestrus. Both the oestrous female and the dominant male advertise their sex and their condition by means of economic but frequent sprays of urine, and any other form of sexual differentiation is superfluous. I have observed a female with a small calf at heel make frequent sprays while threatening another female at a waterhole so the squirting may have a more general link with assertive behaviour.

Owen-Smith (1975) pointed out that the rhinos' peculiar form of territoriality provides a most efficient and economic way of regulating competition for reproductive rights. He noted that at population levels that are close to the carrying capacity of the habitat, territoriality is favoured by a limited potential for surplus food, by relatively sedentary and solitary habits, by the physical risks of fighting, by year-round breeding and by the vulnerability of very prolonged courtship to interference.

Copulation is only effected after the male has thoroughly accustomed the female to his approach and broken down her defensive reactions. Unusual calls, circling and posturing, as well as prodding on her belly and chin resting on her rump, appear to appease her and enlist her co-operation. There are several observed instances of young female *Diceros* behaving towards the male in a manner resembling a playful calf, with active curiosity alternating rapidly with flight impulses.

Although breeding is continuous, there is evidence that mating peaks occur in both species and these have some correlation with the end of the dry

season and early rains, so that a connexion between fresh green growth and the stimulation of oestrogens in the female is possible.

Gestation lasts 15 to 16 months and the young are on their feet in less than half an hour. After a period of some weeks' seclusion within a small sheltered locality, the mother wanders more widely with her young one, who keeps extremely close to her. Females of *Ceratotherium* tend to follow their young, whereas *Diceros* generally lead theirs. The dependence of the young on the mother is total and orphans usually starve unless they are weaned or can form an attachment to another female.

Favourite zoo animals, rhinos are generally not difficult to keep and breed and have a life expectancy of 35 to 50 years.

Black rhinoceros, Browse rhinoceros (Diceros bicornis)

Family Rhinocerotidae
Order Perissodactyla
Local names
Faru (Kiswahili), Kifau (Kisambara), Infwoko (Kingiha), Mbusya, Mbila (Kikamba), Bia (Siha, Chagga), Huria, Munyi (Kikuyu), Mburia (Kipare), Mpuria (Kimeru), Mpenbee (Kinyaturu), Mpembele (Kinyiramba), Mpela (Kitaita, Kizima), Pera (Kirabai), Isabhi (Kijita), Mela (Kihehe), Omuga, Amuka (Lwo), Enkula (Luganda), Muni (Kisamburu), Emunyi (Masai), Enkura (Lunyoro), Ejiji (Madi), Amosing (Ateso), Kipsirikto (Kalenjin), Kurrbatit (Sebei), Kipsirichet (Kipsigis), Kibawit (Elkoni), Warses (Kiliangulu), Weyil (Somali).

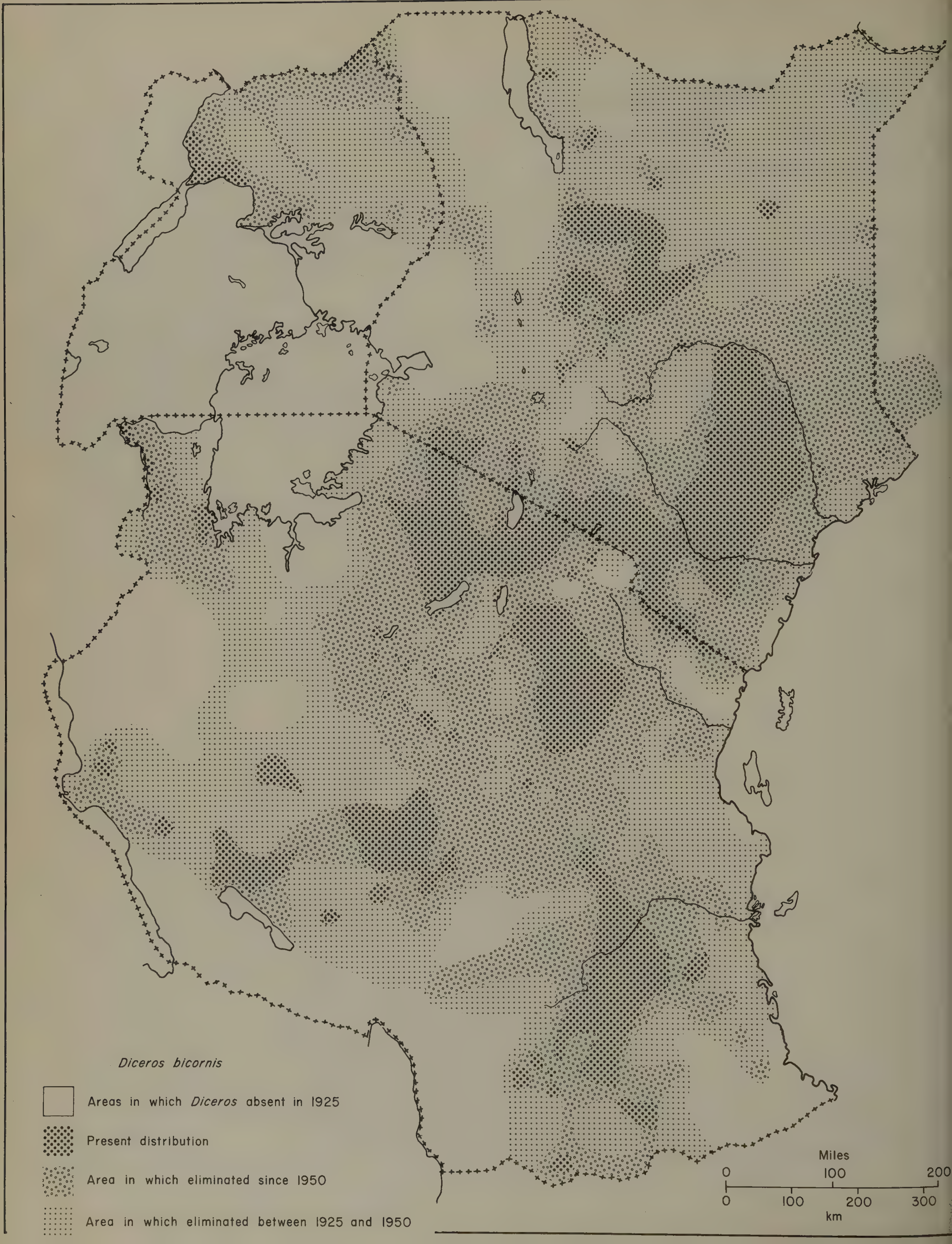
Measurements
head and body
3·4 (3—3·75) m
height
1·66 (1·4—1·8) m
tail
70 cm
weight
996—1,362 kg

Black rhinoceros, Browse rhinoceros (Diceros bicornis)

This rhinoceros is subject to considerable variation, some of which may represent local genetic traits; animals from the more arid habitats tend to be smaller and the highly variable skull proportions may also tend to show some degree of regional consistency. However, it is doubtful if any racial subdivision is justified.

This species probably ranged over a large part of sub-Saharan Africa at one time and it was found in practically all but the very driest areas of East Africa until relatively recently, commonly at altitudes up to 2,700 metres. It seems to be absent from the hot, humid lowland forest belt from Nigeria to Uganda but small population pockets were reputed to exist in the forests of the Middle Congo and Cameroon (Blancou, 1954). Because it needs to drink regularly it is only found within range of permanent water. Although it disperses into a wider area in the rains, its maximum dry season range is about 25 km from water. On open grassland and in closed canopy areas of the *Brachystegia* woodlands rhinos have always been very scarce or absent, and their favoured habitats are along the edges of thickets and wherever there are extensive areas of short woody growth, the thin regenerating twigs of which provide, together with legumes, their main food, however these may be heavily augmented by grass in some marginal habitats. Where there is a permanent source of water and plenty of shrubs and herbs growing within easy reach, the rhinoceros is capable of becoming a major animal in the ecological community because its diet includes resources which are used by few other animals except elephants. The black rhino was therefore very common and widespread until recently and it is still capable of reaching astonishing densities when protected in suitable habitats. In the Ngorongoro crater twenty-three rhinos live in the 2·6 sq km of Lerai Forest, a grove of *Acacia xanthophloea* trees with thin canopy and continuously regenerating undergrowth which provides the animals with ideal conditions. Of these twenty-three rhinos, Goddard (1967a) never saw seventeen outside this area in three years of intensive study. Pointing out its unique dietary niche and ecological role, Frazer Darling (1960a) considered that this animal might be a key species in the management of indigenous African vegetation.

Some 200 species of food plants from 50 families have been recorded by Goddard (1970b) and some of the commonest foods are dominants in the thicket, hard-pan Acacia and riverine communities that are favourite rhinoceros haunts. Thus *Acacia*, *Commiphora*, *Grewia*, *Cordia*, *Lannea*, *Euphorbia*, *Adenia*, *Sanseviera* and *Aloe* are commonly observed rhino foods. Shenkel (1969) also lists *Aerva persica*, *Bauhinia*, *Blepharis*, *Ehretia titensis*, *Sericomopsis* spp. and *Crotalaria*. In spite of being uncommon, *Caesalpinia trothae* is a favourite food; also green clover, *Trifolium*, is greatly favoured while certain dominant plants such as *Boscia* and *Thylachium* are never eaten at all. Salt may be a factor in the rhino's liking for *Suaeda monoica*, a shrub growing in saline soils. Rhinos are soon regular visitors to the artificial salt licks that have been set up beside many tourist lodges.


Diceros bicornis
Areas in which Diceros absent in 1925
Present distribution
Area in which eliminated since 1950
Area in which eliminated between 1925 and 1950
Miles
0
100
200
0
100
200
300
km

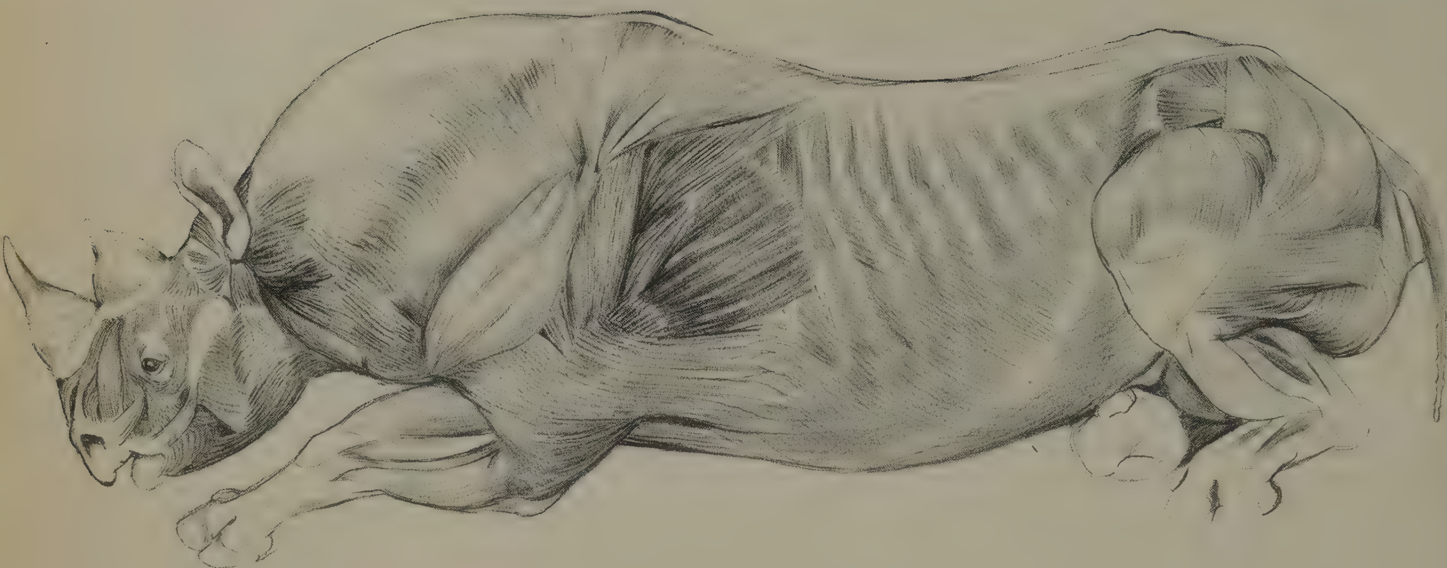
The importance of the prehensile upper lip in gathering twigs into the mouth has been mentioned and it is interesting that rhinos on the floor of the Ngorongoro crater, where grass is normally an important food, took to picking up gnu dung for some days when the grass was only 7—8 cm long following a fire. Klingel and Klingel (1966c) suggest that this may have been to correct a mineral deficiency but, more simply, it may have been due to the difficulty the rhinos faced in cropping short grass. As several hundred gnu were in the area, their dung would have answered the rhinos' need for bulk food more effectively than attempting a task for which their mouths are ill-adapted.

Various fallen fruits are readily picked up and the large sausage-like fruit of *Kigelia* are favoured, as are those of various *Acacia* and *Grewia* species. Roots, particularly those of succulents, are occasionally eaten. The horns have been seen to dig them out as well as to break branches above the reach of the mouth. Rhinos have even been seen to balance on the backlegs to reach twigs nearly 3 m off the ground.

Digging for water is not uncommon in rhinos and in the sand of river beds they use their forelegs quite effectively to this end. Water is needed in some quantity as sweating is the principal cooling mechanism of the rhinoceros. Notwithstanding the habit of hanging around waterholes, they generally drink rapidly and finish in less than five minutes. I have followed rhinos over 10 km back to their regular haunts, which they reached in less than three hours with very little feeding on the way. Well-worn tracks, usually shared by a variety of other animals, lead to and from water to wallows. In areas where many rhinos are concentrated there is a maze of subsidiary tracks running parallel to the main ones. In thickets rhinos can become important pathmakers for other animals if they use a track often enough but many of the plants such as *Lannea* and *Commiphora* are sufficiently pliant to spring back after the rhino's passage. Following a rhinoceros in such country can sometimes mean crawling on hands and knees for long periods.

Resting and sleeping in mud wallows is common, but the heat of the day is normally spent sleeping under shade, while the most intense feeding periods are in the earlier part of the morning and evening. In areas where they are persecuted they become largely nocturnal. Wallowing in mud or water is a conspicuous habit. During the 1960—61 drought when hundreds of rhinos died of nutritional anaemia (Tremlett, 1961), a high proportion ended up in the shallow waters of the Athi River, where they presumably found some relief from the heat and biting flies. Schenkel and Schenkel (1969) have suggested that wallowing protects the skin from flies as well as conditioning it. As wallows are most commonly used during or after the hottest part of the day, cooling is likely to be the most direct incentive for the individual's behaviour. Incidental effects might include protection from sun and insects, also the blazing of pathways with flakes of scented mud, which are probably valuable identity tokens for the scent-orientated rhinoceros.

Rhinos so frequently pass under or through bushes when they could just as easily have skirted them, that one suspects that scraping and scratching must be a rewarding sensation for the animal; shedding flies and mud flakes could be incidental benefits of this behaviour. As well as using mud wallows, rhinos will roll in fine dust or the ash of burnt trees or branches. They are



often attracted by bush-fires and have even been known to scatter burning logs with their horns. I once found the impression of a rhinoceros that had rolled in ash so perfectly recorded that the animal could be recognized by its scars and creases. Such impressions also show that the depression immediately behind the shoulder may miss being coated in ash or soil. As this spot is the commonest area for "rhino sores" the protective function of mud and ash seems evident.

Exposed areas of skin are very thick and inflexible—the effect is of armour plates. Between these plate units movement demands more flexible and thinner skin and lions attacking rhinos have been seen to seize the throat and chest, after which they can easily unbalance the top-heavy animal and bite the softer underparts.

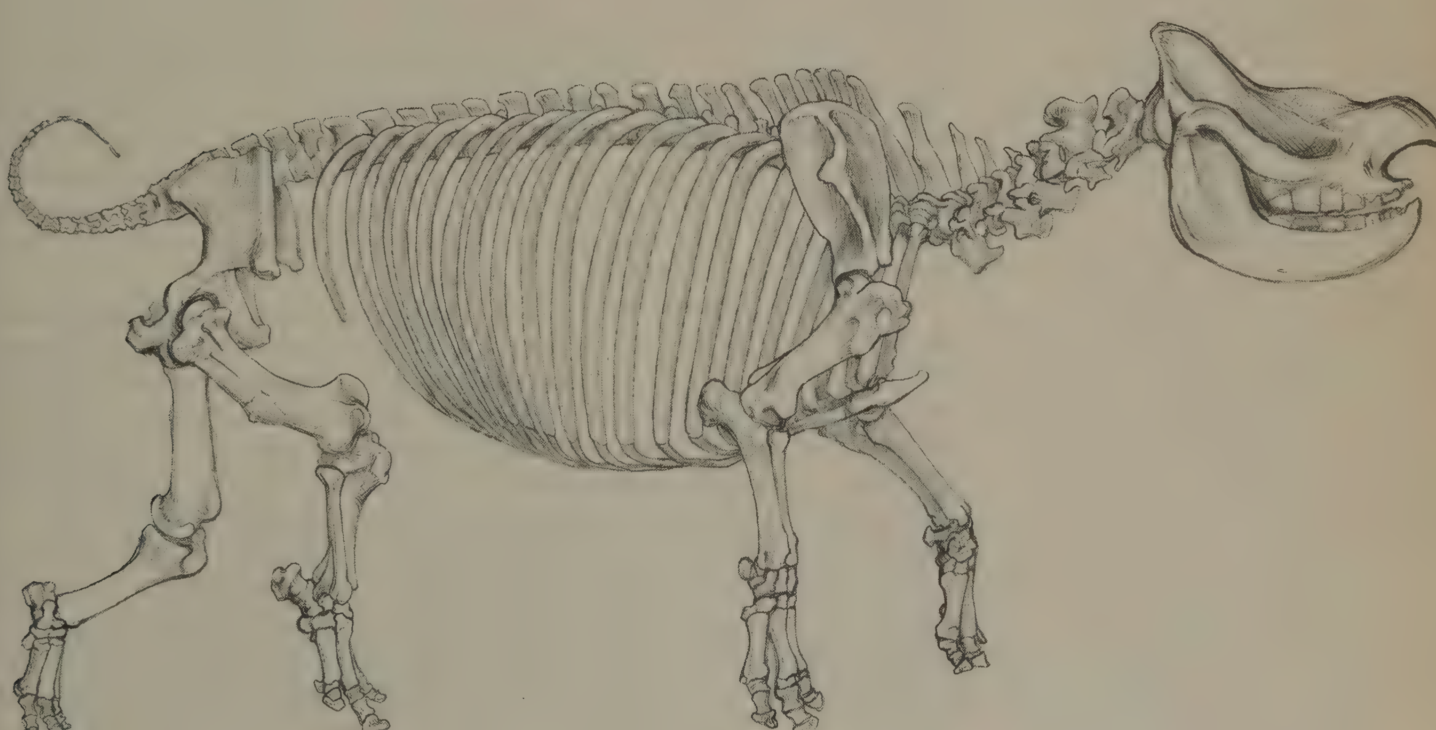
Rhinoceroses cannot roll across their sharp spines from side to side but lie down with hindquarters resting on one leg and then roll sideways until the spine throws them back. They will generally half rise or even get up and turn round before rolling on the other side. Abrupt rising and a few brisk movements, even interrupting a period of complete immobility or preceding a long sleep, are characteristic of rhinos. A rhino may sleep lying on its brisket, chin or cheek on the ground or it may doze standing with its head hanging. The ears continue to move even when it is asleep.

Rhinos are not slow and can make sharp turns even in the middle of a charge at some 50 km per hour. An alerted rhino tries to focus its ears on a source of alarm and may swing from side to side with the head up and nostrils flaring as it sniffs.

Although eyesight plays an inferior role to hearing and smell, the common claim that rhinos are half blind is misleading. Long-distance vision is of little importance to them but they give every sign of responding to visual stimuli at

close quarters. In some encounters, swinging movements seem to have the character of ritualized head-flagging. Bulls, particularly, raise their fore-quarters in a stiff-legged walk with erect head, in which they turn with some deliberation and posture in profile. It has been suggested that this is in order to see better out of one eye than ineffectively out of two, but head-on vision is functional in spite of a broad muzzle and horns (see drawing). However, myopic the rhinoceros seems to be, it is certainly capable of perceiving the silhouette of a massive neck, head and horns. Bulls tend to meet at wallows and waterholes and encounters are characterized by mutual displays which may or may not develop into sparring matches.

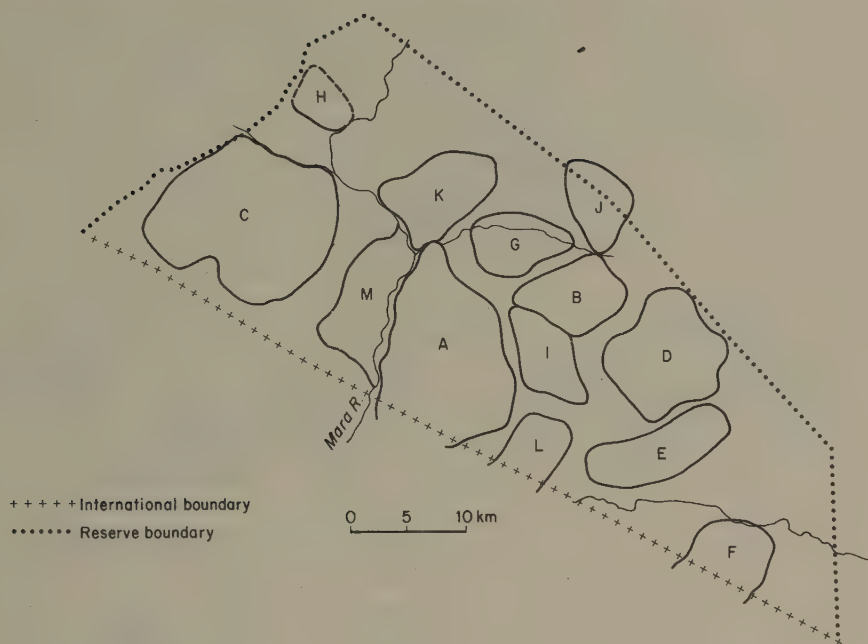
Alarms and threats are accompanied by short snorts but it is evident that snorts probably have shades of meaning for the rhino. A male approaching a female punctuates his slow progress with a series of three or four snorts, pausing momentarily after the first before giving two more in quick succession; the effect is somewhat like morse. When excited they also make a deep wheeze, which has been likened to a man gasping for breath. I have heard a similar call in a captive when approached by his keeper; it may imply pleasurable excitement or it could be an adult modification of the high-pitched noises of very young rhinos at play. These are different to the squealing distress call of the young. During his immobilization and tagging programme, Goddard (1970a) witnessed a calf attract an adult male from over a kilometre away in response to its squealing. Another very high-pitched call is uttered by mothers calling their young. When threatening or fighting one another, rhinos grunt loudly or else scream.



Like many other mammals, male rhinos scent the boundaries of their home range with urine. Bushes, tufts of grass, stumps or stones are sprayed with a scattering of urine drops which dry out into white flecks. These landmarks are generally temporary but Ritchie (1963) and others have reported that a hard deposit similar to the "dassiepiss" of hyraxes may form on rocks that are used for many years, possibly by generations of rhinos. This habit is mainly an adult male's prerogative and the penis is well adapted to direct a horizontal squirt between the hindlegs. Females make a finer spray while they are in oestrus or during encounters with other rhinos in the presence of their young, but it appears to be at random (Schenkel and Schenkel, 1969). These authors report that in the early mornings some bulls may make a more or less circular tour sniffing and urine squirting. Rhinos also use well established dung deposits, some individuals wiping their hindlegs through the dung immediately afterwards. Single deposits are common on roads and paths but these may represent no more than the reaction of animals encountering a strange element in their surrounding. The cumulative dung middens, however, tend to be added to by rhinos of either sex that come across them. Mukinya (1973) found a relationship between the degree to which a pile was shared (and hence its size) and the frequency with which a path or area was used by other rhinos. The social nature of dunging behaviour is betrayed by young rhinos that soon follow the mother's example. Sheldrick, who reared a young rhinoceros, could make it defaecate by scraping the earth with his boots.

As with many scent-oriented animals, an important function of these deposits may be connected with reassurance within the home range, by extension of the "self"and may favour the regulation of social and sexual contacts by allowing animals in the same area some choice in contacting or avoiding one another. Both these functions are well illustrated by Goddard's experiments in Ngorongoro while he was trying to learn more about the significance of scent trails. He dragged bags of rhinoceros dung behind a vehicle, laying out complicated trails for distances up to two miles. Most rhinos were able to follow every twist and turn of the bag, 60% of them followed their own dung trail and most of them chose to defaecate on it and an even larger proportion, 70%, followed the dung of animals with which they shared the home range. However, only 20% of them defaecated over it. The least response (30%) was for the dung of distant rhinos.

Goddard (1967a) was unable to find any consistent pattern in the deposits of dung, which are apparently random in distribution. Urine on the other hand, may be the main way of marking out the area used by an individual. Rhinos, particularly adult males and particularly in dense habitat, are essentially solitary but Goddard (1967a), noting their tolerance of well known neighbours, described the rhinos resident within a restricted locality as a community. Joubert and Eloff (1971) have used the word "clan" and they regarded a watering point as the focus for all social activity. In such circumstances rhinos are often tolerant of one another. In a study of the ecology and behaviour of 108 black rhinos in the 750 sq km of the Masai-Mara game reserve, Mukinya (1973) was able to delineate thirteen areas of variable size, within which resident rhinos associated with each other but were never seen

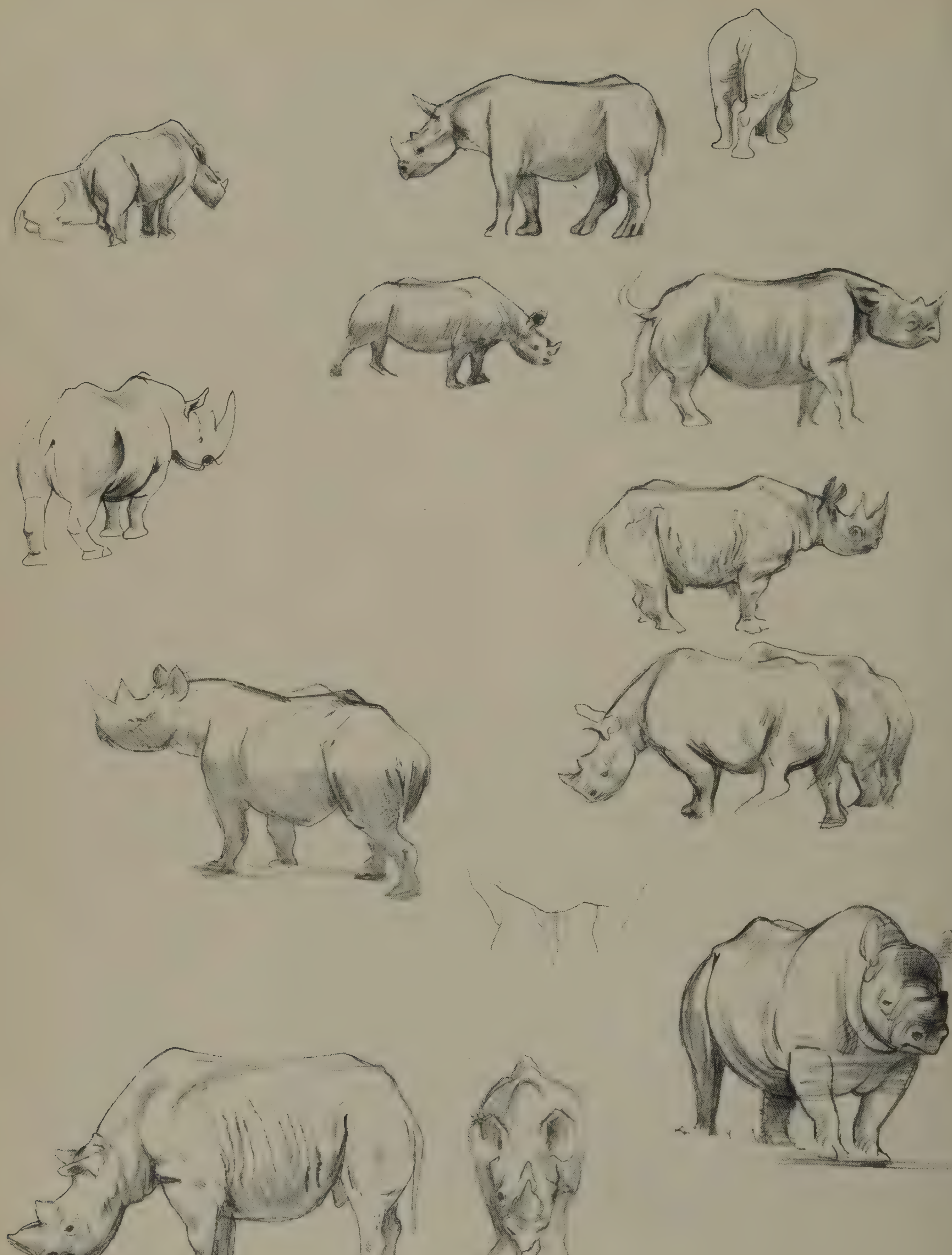


Rhinoceros distribution or "clan" areas in Masai Mara Game Reserve, from Mukinya (1973).

with individuals from another area. As many as thirteen have been seen together in a wallow in Ngorongoro but such aggregations are very temporary and soon disperse into singles and groups of two or three. Female rhinos are hardly ever alone. Most of their life is spent with their current offspring, sometimes in company of an earlier daughter. If without any young, females form attachments with neighbouring females. When the long-sustained bond between a mother and her offspring is broken by the birth of a new calf, the subadult rhinoceros is quick to seek out a new attachment irrespective of its sex. At this stage subadult rhinos range over a larger area. Occasionally a rhinoceros disturbed by a vehicle gives the impression of actively seeking contact with a large moving object. This was noticeable when a solitary subadult animal that had recently lost its mother tried to follow my Land-Rover.

Only when they are fully adult do males become solitary and even then they may associate with other neighbours for variable lengths of time.

In Ngorongoro, Goddard (1967a) thought adults of both sexes had similar-sized ranges and estimated an average of about 15·5 (2·6—44) sq km in open grassland, a third of which was regularly shared with other rhinoceros. In the more barren Olduvai gorge, the average was about 25 (3·6—90) sq km and males appeared to have slightly smaller home ranges. Comparing a well-thicketed area with more open savanna in South Africa, Hitchins (1969) found similar orders of magnitude with many more animals living within



smaller ranges in thickets. After marking all the resident rhinoceroses, Goddard was able to affirm that conflicts between males in the crater usually concerned strangers wandering into an established range and that strange females were not treated as violently as males. Nursing females were found to have larger ranges than single females or single males by Mukinya (1973). He recorded an incident in which one animal snarled and screamed at another which simply stared, after which both animals ran off in opposite directions. It was perhaps in cases where the invader was dominant that Goddard saw resident animals scream and snarl at a silent stranger. In one instance the intruding bull from another area displaced a resident male, which in turn moved into a neighbour's range, illustrating what might happen when the status quo is upset by ecological or other disturbances. A chain of displacements might have been a factor in the situation reported by the warden of East Tsavo shortly before the 1960—61 drought, when all the rhinos seen in that area were covered in fresh wounds and a number died as a result of fighting.

Fighting over females has been reported but it is also known for several bulls to court a female without conflict and Schenkel and Schenkel (1969) considered that there is not very much direct competition for oestrous females. Males do not associate closely with females except while they are in oestrus.

Watching the Tsavo rhinos during a period of drought, Schenkel and Schenkel (1969) thought that the females were generally intolerant of one another. However, in certain circumstances they seem capable of giving one another some degree of mutual protection. Ellis (1958) saw four rhinos come out of a forest together and cross a plain. "Three of these fully-grown rhinos were moving in a strange manner, pressed shoulder to shoulder, with the fourth one following behind. On closer inspection it was seen that the three front ones were cows, and that the centre one, very heavy in calf, was being helped along by her companions. One of the attendant cows actually rubbed the pregnant animal's flank with the side of her head and horn. Rangers reported the birth of a calf three days later." Perhaps pregnancy elicited maternal or protective responses in the other females but, unusual though it is, this observation serves to show that apparently altruistic social behaviour is not unknown in black rhinos.

Births are about two to four years apart and Klingel and Klingel (1966) estimated that about 28% of the Ngorongoro females bred each year. Births have been recorded at all times of the year but mating peaks have been suggested for September—November and also for March—April in Kenya. The gestation period is about fifteen months, 446—478 days.

Courtship has sometimes been described as being phlegmatic and without display but it is not unusual for the female to attack the male and he is often very slow and circumspect in his initial approach and movements. More than one male has been seen to try and court a cow, pairs form and break up very easily and Cowie watched a male copulate with two females in succession. Goddard, however, saw one pair associate for four months after mating. Males make a distinctive display towards females, which Schenkel and Schenkel (1969) have interpreted as symbolic aggression against a rival; it consists of sideways swipes with lowered horns directed at the ground or at a

bush, short forward and backward rushes on stiff legs accompanied by the shuffling and scraping of the hindlegs that normally accompanies foot-scenting together with urine-squirting. Schenkel and Schenkel have also described a young female becoming very excited as she repeatedly approached and fled from a big male only to return again and repeat her approaches. Another observer in a car also interrupted a courtship in which the female appeared to take an active role. The precipitate flight of the male had passed unnoticed by the female, which continued for about fifteen minutes to display towards the motionless car. After a retreat brought no response, she stopped and pranced; then she took a tuft of grass in her mouth and tossed it into the air. After approaching closer with a stilted walk she suddenly caught the scent of the car and charged into the vehicle's bumper.

Circling the female, the bull may prod her belly with his horn, curl back his lip in a spectacular *flehmen* gesture and lay his head on her back before attempting to mount her, standing in an upright posture and keeping up with her steps. Copulation may last over half an hour and may be repeated intermittently over a few days.

The birth of a wild rhinoceros was witnessed by Park Scouts Edy and Malinda in Manyara National Park. They had been descending one of the game trails along the rift wall when they found a female rhinoceros lying down in their path:

> "thinking the animal was probably dead, they first threw some stones in her direction, with no result. They approached closer and found the surrounding ground was covered with liquid. Within a few minutes the rhino got up and with little effort the calf was seen to appear. Within approximately ten minutes, the calf was dropped. The mother then turned round and started removing the birth sac with her mouth and ten minutes later the baby was on its feet, twitching its ears." (T.P.R., 1961).

Mothers are extremely intolerant of any disturbance for some days after a birth and it is probably at this stage or just before the birth that the former calf is driven off. The new calf is about 40 kg at birth and sucks within three hours. Twin calves are unknown but it is possible that adoptions take place. Thereafter the calf sucks briefly but frequently. Schenkel and Schenkel noticed that mothers with recently born young avoided wallowing even though the wallows are preferred areas for suckling. The young bleat for their mothers and continue sucking when they are so enormous it is necessary for them to lie down to get their heads under the mothers' bellies. They keep very close indeed to the mother and respond to every detail of her behaviour. Normally the calf follows but in an alarm the mother attempts to interpose herself between the baby and the cause of alarm and she tends to swing broadside on to the source of the disturbance, which hides the calf more effectively. Both animals tend to get their backsides together and as the calf gets older this behaviour turns into a very characteristic radial formation with which any group of subadult or adult rhinoceroses first responds to an alarm.

Very young calves can be quite frolicsome and will rush around tossing vegetation. Frame (1971) watched three calves taking turns at picking up and mouthing a stick without biting or chewing it.

Although it becomes independent at about two-and-a-half years a rhinoceros is not fully grown until about seven. However, it is sexually mature between five and six. Ages of about forty years have been reached by zoo animals and the animals are probably fertile to the end.

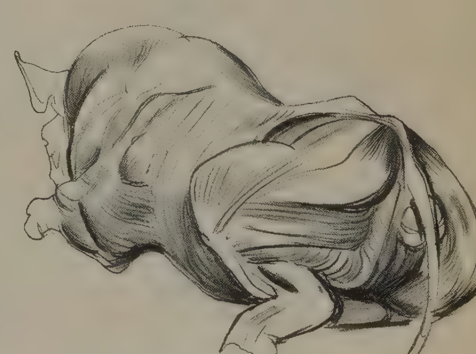
Goddard (1970a) estimated an annual mortality of about 16% in the first two years of life, dropping to 9·8% between the ages of five and twenty-five. Recruitment in Ngorongoro is about 7% but it would be difficult to find a truly undisturbed rhinoceros population today and all the results of population dynamics must be calculated in the light of very local conditions.

In their preferred thickets rhinoceros are impossible to count accurately over large areas but Goddard (1969a) used density strata samples to estimate 6,000—9,000 animals in the Tsavo National Park. This is the largest single concentration of the species in existence today (Glover and Sheldrick, 1964). At the time of this estimate the area also supported about 36,000 elephants. While the elephants had increased over a period of some twenty years, Sheldrick considered that the rhinoceros population had fallen by half over the same period. It would be extremely interesting to learn more about the interaction of these two species and see how elephants might influence the numbers of rhinos and this should be one of the priorities for wildlife research in the region.

Where rhinos are numerous, their young and very occasionally adults may fall prey to lions, and hyaenas have also been known to kill young rhinos. Elephants, hippopotamuses and crocodiles have all been recorded killing rhinos but these are almost as isolated as the instances of rhinos attacking other animals. When resistance has been lowered by lack of food or water, disease may hasten death, but there is no evidence of rhinos suffering from widespread epidemics.

A large number of tick species and other parasites have been recorded from rhinos (see Zumpt, 1964) and the "rhino sores" found behind the shoulder are associated with a worm, *Stephanofilaria dinniki* (Schultz and Kluge, 1960), which is carried by flies and ticks. Two species of flies, *Rhinomusca* and *Lyperosica*, develop in rhinoceros's dung and, after hatching, fly on to the first rhino visiting the dung midden.

Because the rhinoceros's favourite habitats are generally well-watered and reasonably fertile, settlement of rhino habitats is continuous. When food or cotton crops are damaged, or herdsmen are chased there are demands for control or extermination. Very large numbers of rhinoceros have been killed on the assumption that any form of human enterprise and the presence of rhinos are incompatible. One hunter, a former Scottish gamekeeper, claimed to have killed 1,600 rhinos in Kenya, most of them shot officially in order to make way for government settlement schemes. It is impossible to know how many rhinos have been killed illegally for their very highly priced horns, but a fairly detailed reconstruction of the species' overall decline in East Africa has been possible (see maps).

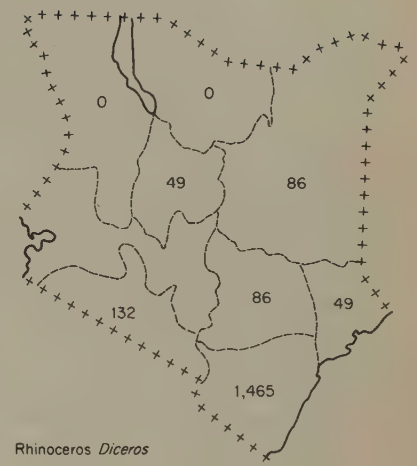


The varied disposition of rhinos is in the opinion of Ritchie (1963) related to genetic selection over many generations of exposure to hunters or to the greater tolerance of pastoralists. Given the long period of learning, it is more likely that the killing off of rhinos that expose themselves to attack has favoured those that have acquired a learnt tradition of caution and/or

truculence. The traditional attitude of Masai pastoralists towards rhinos resembled that of European country folk towards dangerous domestic bulls, avoiding provocation and giving due respect to their size and armament, and it is no coincidence that the largest populations of rhinoceros still left outside national parks are in Masailand (see map).

Although they are effective converters of very coarse, prickly vegetation into animal protein, they are not very suitable for regular exploitation as meat, among other reasons they grow and breed so slowly.

It is important that the species be conserved wherever possible and the details of its ecological niche be investigated further; for fossils have shown that black rhinos have been an important part of the African scene for several million years.



Preliminary estimate of *Diceros* numbers in Kenya rangelands in 1977. From Ministry of Tourism and Wildlife, Kenya Rangeland Ecological Monitering Unit. Aerial survey report No. 3.

White rhinocerus, Grass rhinocerus (Ceratotherium simum)

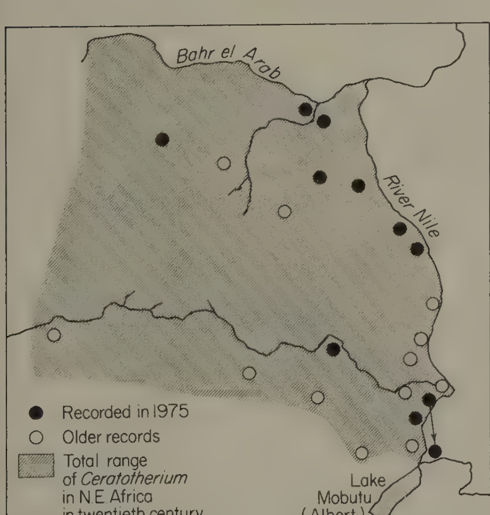
Family Rhinocerotidae
Order Perissodactyla
Local names
Kifaru ya majani (Kiswahili), Ijiji (Madi), Ubirya (Lugbara).

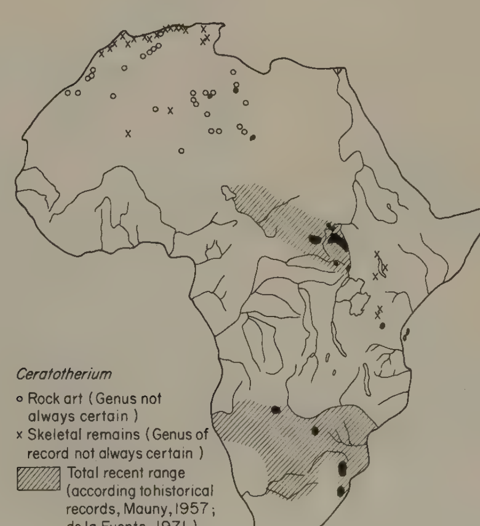
Measurements
head and body
3·6—4·2 m
height
1·5—1·85 m
tail
48 cm
weight
2,300—3,600 kg
horn
95—101 cm (Northern population)
95—200 cm (Southern population)

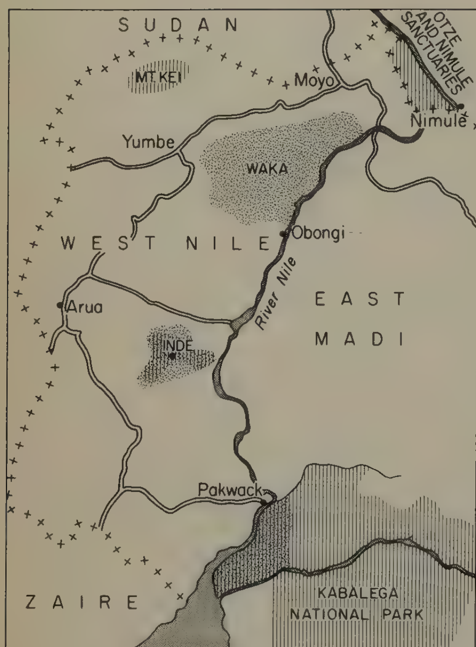
White rhinocerus, Grass rhinocerus (Ceratotherium simum)

The survival of this huge grass-eating animal, second only to the elephant in size, in two widely separated pockets, one by the Nile and the other in Zululand, has been the subject of much discussion. The two populations have been regarded as racially distinct mainly on the basis of the relative concavity of the skull forepart. Cave paintings from as far afield as the Sahara, the Kalahari and Tanzania show that this species had a very much wider range within very recent times, although it was already greatly reduced before Europeans started exploring the continent.

The common black rhino was known to Linnaeus in 1758, whereas the white rhino was not described until 1817 from South Africa and 1907 from Uganda. What made this animal so scarce and why has it survived in these two areas? Like all rhinoceroses it needs water (for example, many died in Zululand during a drought in 1932). Also, the grass rhino eats a lot of food; the sheer quantity needed by each rhino might be difficult to obtain during droughts, both because the vegetation has died or been burnt off and because smaller ungulates with bigger ranges, faster or more efficient cropping methods and greater numbers might converge on water supplies and compete for reduced resources. Thus areas subject to erratic rainfall have perhaps always been avoided by this species. As grazers forest, dense woodland and thickets would also have been closed to them. Recolonization of lost ground is delayed by the slow breeding and static habits of these rhinoceroses but, even allowing for this and considerable fluctuations of climate, large areas of Africa, between the two extremes of forest and semi-arid country, should have been available to grass rhinos for they do not demand very special grass species or extraordinary ecological conditions. They are almost immune to wild predators and it is perhaps this invulnerability that has encouraged a







Above: Gazetted white rhino-sanctuaries and National Parks in North-west Uganda and present range of *Ceratotherium*. Introduced into Kabalega National Park. Eliminated in Mt Kei and Otze sanctuaries. (Also exterminated in Nimule National Park, Sudan.)

Right: Ungazetted refuge for *Ceratotherium* in area of Waka seasonal swamp.

Seasonally flooded *Hyparrhenia* grassland with scattered *Combretum* and *Acacia*

Seasonally flooded *Echinochloa* grassland

Papyrus swamp

Dry *Combretum* wooded *Hyparrhenia* grassland, scattered *Acacia*

Wet season concentration areas on better drained soils (sometimes on abandoned fields) grasses are *Chloris*, *Eragrostis*, *Digitaria*, *Loudetia*, *Cynodon*

Settlements

Ajai's White Rhino Reserve, Inde, Uganda

fatal tameness. In 1927 Pitman visited West Madi and described walking within 3 m of them. In no single instance did an animal show any aggression towards him, although the rhinos were aware of his presence and were watching him with interest. In such circumstances an animal is exceptionally easy to kill, even with the most primitive of weapons and there is no doubt whatever that hunting has been entirely responsible for their decline and continues to endanger present-day populations. Furthermore, if we turn the coin, it is possible that their survival both in Zululand and West Nile was assisted by the traditional attitudes of the local people. In the former area, the flesh is regarded as dangerously inedible and in Uganda a formerly sparse human population tended to avoid the malarial rhino habitats. In 1924 Game Warden Salmon was told that the rhinos were scarcely ever molested in West Nile prior to the demand for their horns.

Because their habitats are so restricted today it is difficult to be certain that these are representative or even include optimum ecological conditions for the species. Their present refuge on the seasonally waterlogged margins of the Nile is possibly less favourable than their former haunts on the higher ground around Moyo, Kei and Inde Hill. Brooks (1959) noted limited seasonal movements in West Madi, the rhinoceroses moving further inland and on to the hills during the dry months of January and February. At this time the dominant tall grass species of this area, *Hyparrhenia*, *Themeda* and *Setaria* are short tufted after the fires and are, therefore, suited to close grazing and are also at their most palatable stage. Once the rains have started, the rhinoceroses avoid the tall grasses and Brooks found them concentrated in July (the wet season) on short grass meadows. *Digitaria*, *Cynodon dactylon*, *Heteropogon contortus* and *Chloris gayana* are grazed at this time. Other species recorded are *Brachiaria brizantha*, *Urochloa* spp., *Eriochloa*, *Panicum* and young *Phragmites*. The cropping of short grass is not entirely unselective and Foster (1967) noted that they were not eating the widespread *Sporobolus festivus* during December and June.

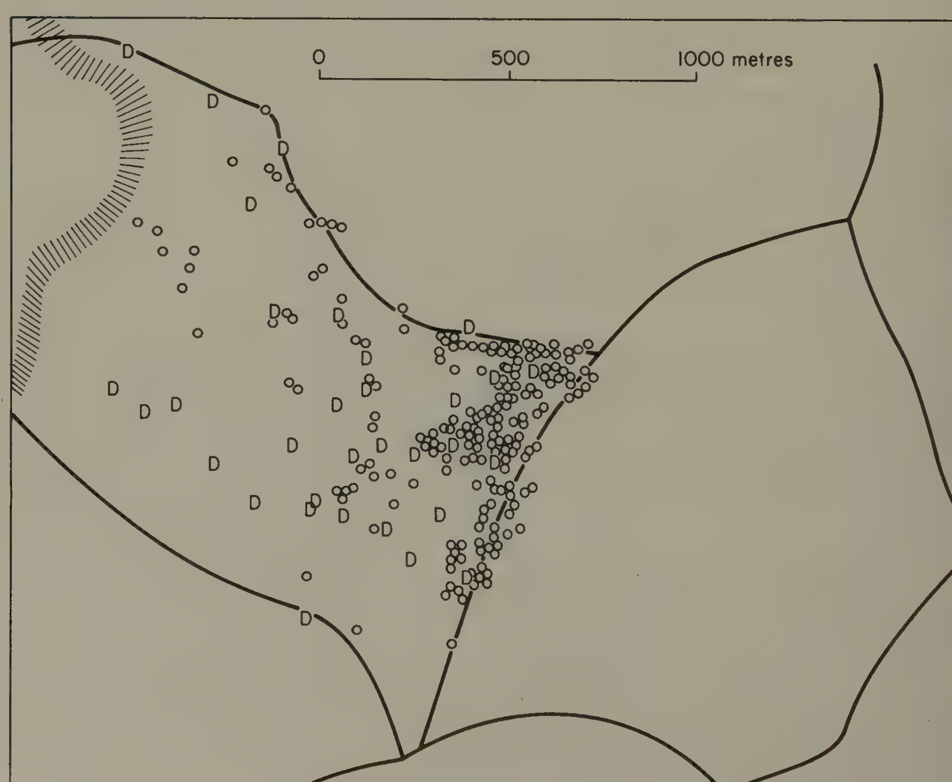
Although they prefer grass shorter than 10 cm they will crop grass up to one metre high in the absence of anything shorter. In addition to grass they may occasionally eat small shrubs and, in Zululand, Foster (1961) noted them commonly feeding on dwarf *Euphorbia*, *Stapelia* and a creeper, *Sarcostemma viminale*.

Grazing is generally sustained for a few hours and alternates with resting spells. This may continue throughout the day and night in cool weather, but the midday rest becomes progressively longer as the dry season advances. Several observers have noted a tendency for these rhinos to congregate on exposed ridges during the middle of the day, even neglecting to use available shade and it is possible that biting flies may influence this behaviour as harassment is worse along watercourses and near thicker vegetation. Foster (1961) suggested that wallowing habits were influenced by the prevalence of flies, but temperature regulation is clearly the most important factor and Owen-Smith (1975) noted that wallowing became more frequent in hot weather. Wallows are most readily formed on hardpan soils and rhinoceroses join warthogs and buffalo in maintaining short grass patches on these pans for much of the year; walking from one meadow to the other along well established paths.

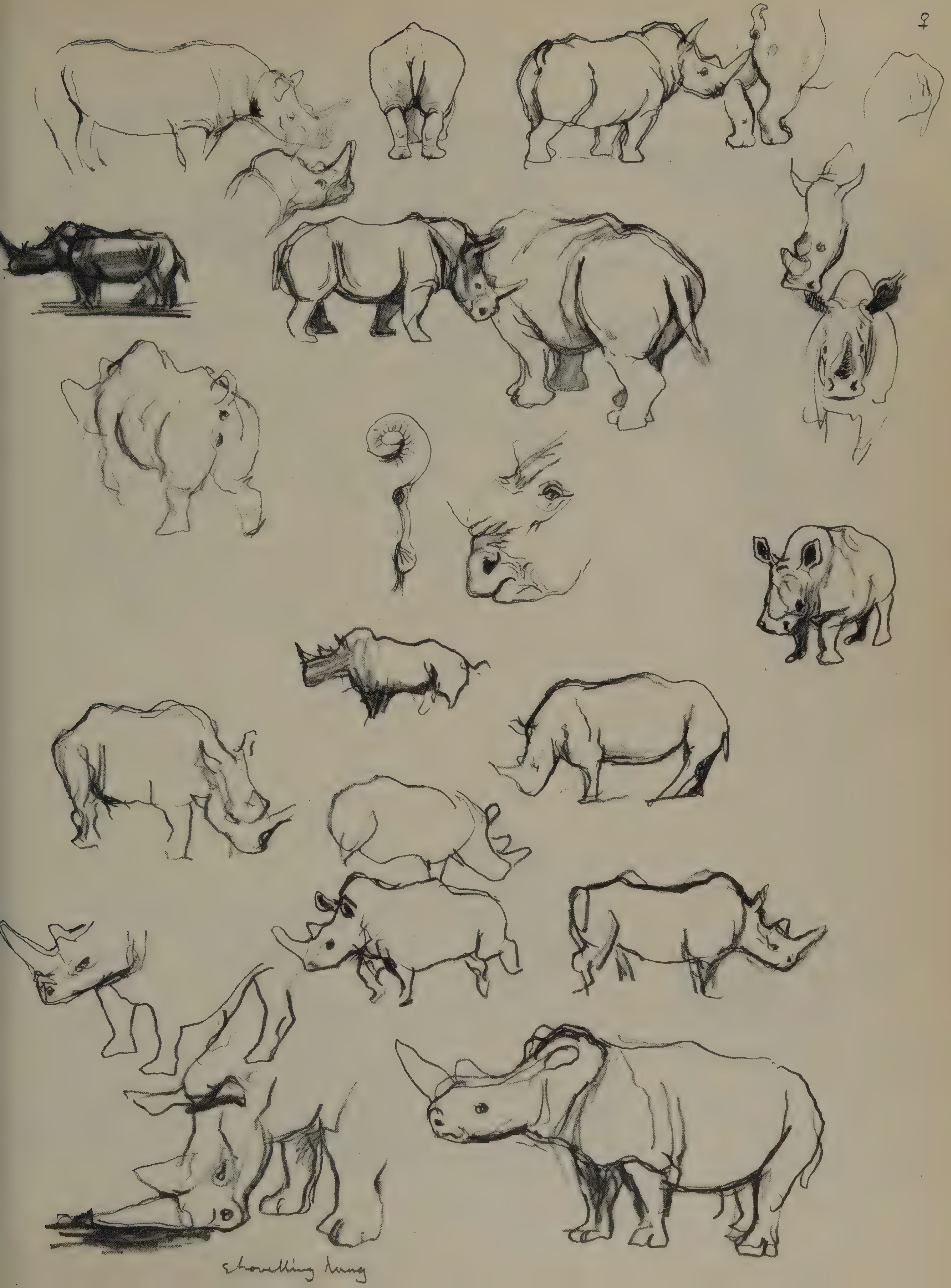
Water is needed every two to four days and very regular drinking habits are attested by well worn paths leading to their drinking stations. In the dry season water may lie 10 km or so from the home range.

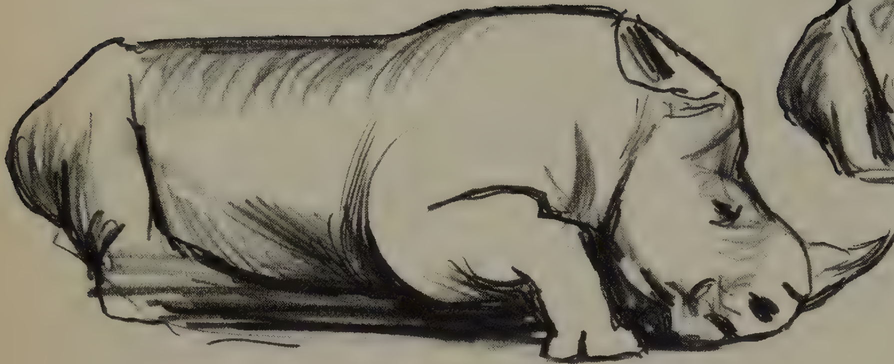
While the rhino is grazing, the head hangs vertically and only during excitement is the head raised very high, causing a tight constriction at the back of the short neck, which gives this species a highly characteristic neck hump. Even when it is running, the head is not carried very high. Galloping is moderately fast, about 40 km per hour, but cannot be sustained for very long and Foster (1961) described Zulu dogs soon winding them in a chase. While attempting to immobilize rhinos in Zululand, Player (1967) had a horse tossed into the air by a rhinoceros and a captive showed considerable agility in climbing over a gate 2 m high.

Scent, as with all rhinos, is very important and dung middens are conspicuous throughout country occupied by white rhino. Rhinos tend to add dung to an established deposit but dominant males only use a limited number of deposits which according to Owen-Smith (1975) average about thirty to a territory. Here the bull kicks and scatters the dung pile every time he uses it, whereas other classes do not disturb it. While the dung deposits are scattered throughout the territory, urine sprays are instead essentially boundary markers and Owen-Smith recorded an average of ten sprays per hour. The dominant male also makes scuffling scrape marks along his boundary trails as well as on any other favourite paths but Owen-Smith found the boundary scrapes were more frequent (one every 28 m instead of one every 38 m).



Distribution of urine sprays (O) and dung piles (D) in a grass rhino territory. (After Owen-Smith, 1975.)


♀
shovelling dung

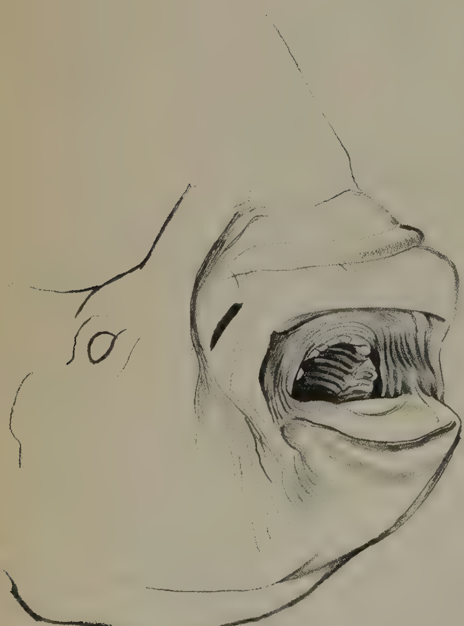


Rubbing posts are also used regularly and I have the stump of an ebony tree, picked up in West Madi, that has been rounded and polished through the regular abrasion of rhino buttocks. They also wallow regularly and occasionally roll in dust.

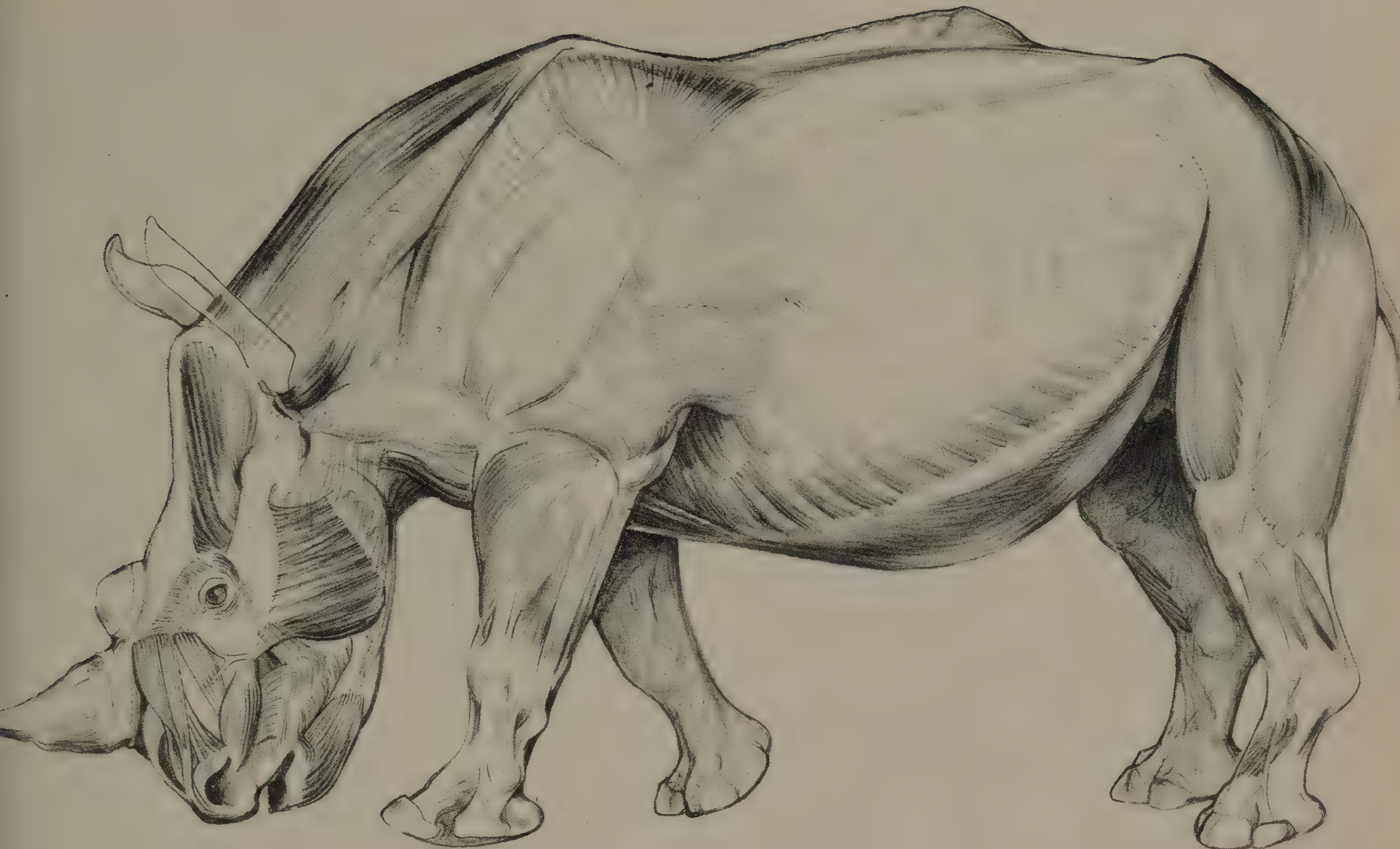
Their vocabulary includes a panting contact call which is common in groups, a squeal of distress and a whining want call in juveniles. Threat is implied by a deep bellow or rumbling growl and inferior animals on the run from others utter peculiar chirping cries, which probably signify submission. A loud wail is made by a courting male trying to restrict the movements of a female and Owen-Smith (1975) described the courting call of an approaching male as "hic-throbbing".

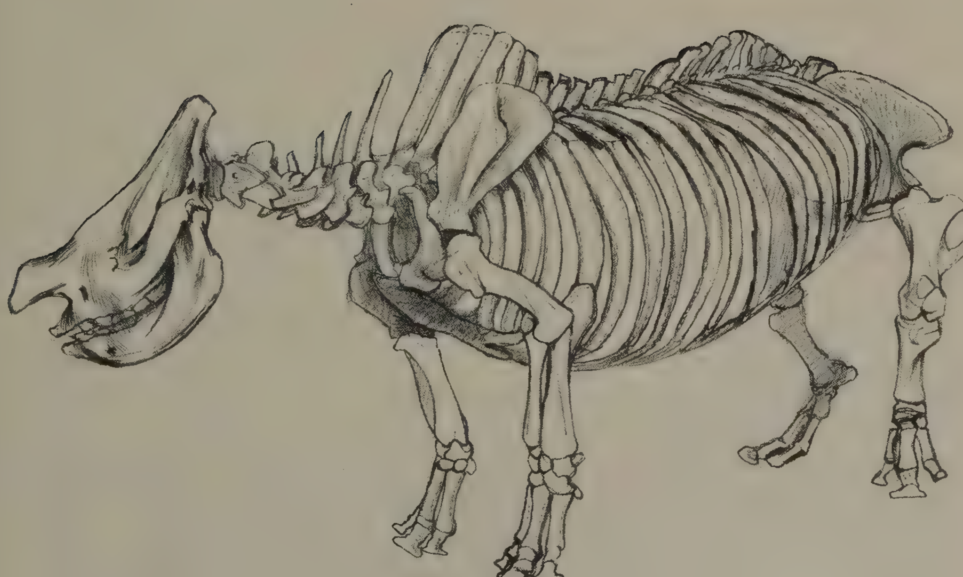
Owen-Smith (1975) summarized the interactions of the various classes of rhinos as follows. An alpha male usually approaches any other rhino within his territory but avoids contacts of any sort outside it. Females are sniffed at, subsidiary males are commonly confronted with a brief apposition of horns while intruding males face a more prolonged confrontation if they do not retreat. However fights are rare and it is almost invariably the resident alpha male that moves off first. Females and subadults are remarkably indifferent to one another but playful horn wrestling is common in these classes as well as in calves. All rhinoceroses, except the very young, tend to respond to the approach of an alpha male with snarling threats, which Owen-Smith saw as "separation maintaining displays". In this display the lips are retracted from the open mouth, the head is raised and the ears held back. A loud snarling roar rises to a shriek if the alpha male makes any threatening movement.

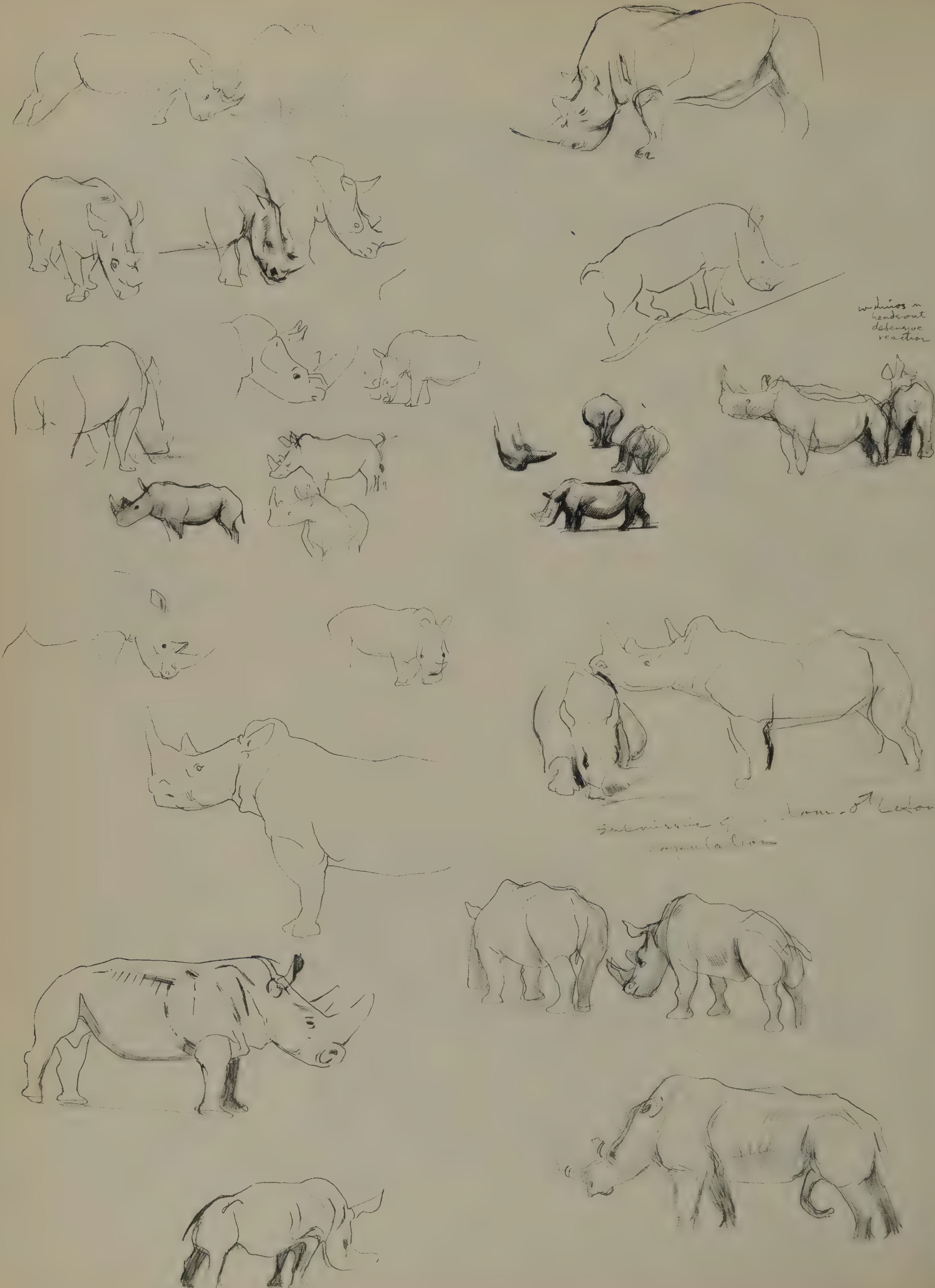
Owen-Smith explains the function of snarl displays as follows:



"Subtle visual gestures of submission are likely to pass unnoticed by a rival endowed with such poor vision. Running is energetically highly expensive in so large an animal, and furthermore exposes the fleeing animal to attack from the rear unless it is capable of outdistancing the pursuer (notably only subadults or young adult males respond by fleeing). There is no safe refuge to which a beta male can retreat, on adjoining territories he is likely to be challenged by other alpha males and there is no unclaimed ground. A beta male's best strategy is accordingly to stand his ground ready to deflect attacking moves by the challenger, repeatedly assert non-challenge and wait until the challenger tires and goes away."






w. rhinos in
heads-out
defensive
reaction

In the Zululand Park, where the very numerous rhinos have virtually no space for their expanding population, Owen-Smith (1975) found land divided up into a mosaic of single male territories averaging 1·65 sq km (0·75—2·60) with very narrow overlapping margins. Territorial males patrol their boundaries and reinforce them by challenging any male that contests them. At the time of Owen-Smith's study as many as a third of the adult males were each living under the subordination of one or more territorial bulls, tolerated within the territories for as long as they gave way to the owner. Except for the period of oestrus females and their young wander freely over the male territories. For example, one territory in Zululand was visited by a total of twenty-six different females (Owen-Smith, 1975). However, females also tend to live

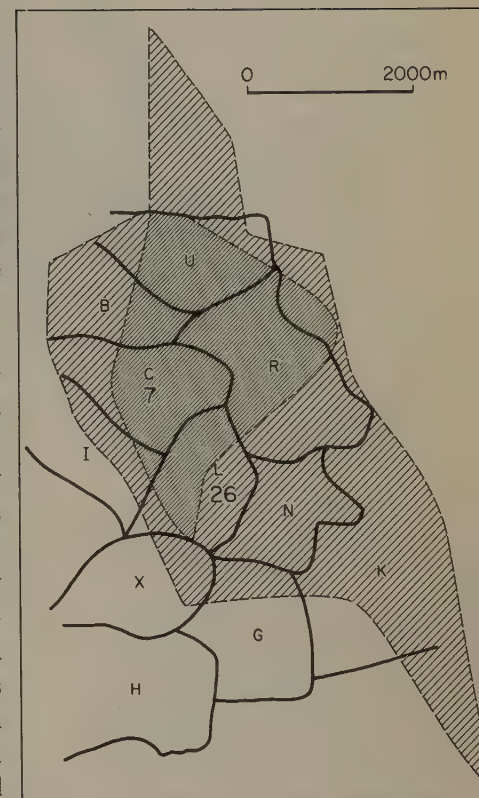
Aggregations of more than two or three animals are commoner in this widely, but others tended to range over an area of only 4—10 sq km. within a limited area of about 10—12 sq km but do not defend land and they share good grazing with other animals. Their normal home range overlaps that of several other cows with their attendant young.

The subadult young are driven off by their mothers at the birth of a new baby, whereupon they tend to pair up with an age-fellow in a similar condition and preferably of the same sex. Alternatively, they may join an unattached female, which occasionally acquires more than one satellite in this way. Many of the adolescent rhinos studied by Owen-Smith wandered species than in the black rhino and they usually centre on wallows, water or a choice area of grazing. Owen-Smith noted that subadult rhinos oriented towards groups rather than to individuals so that cows with immature young are a natural but temporary social focus and may be accompanied by up to six subadults. Of more stable associations lasting a month or more over 40% were with other subadults and 21·5% with a single cow. Only 2·7% of all subadults sighted were solitary; 0·4 cows were solitary, whereas 61·6% of alpha males and 91·8% of other males were on their own. Bonds between mothers and female offspring last longer than with males and Owen-Smith (1975) calculated an average of 10·3 months for the former (with a maximum of 26 months) and 8·1 months for the latter.

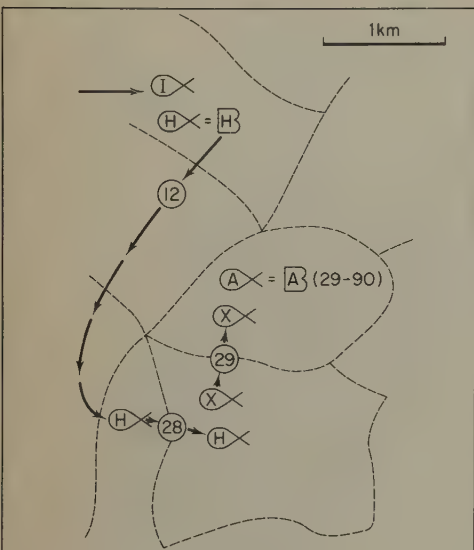
The large grazing ungulates share a general tendency towards greater sociability. Aggregations probably help maintain grass in a condition suited to regular cropping. Rhinos may be favoured by the presence of other grazers as long as grass and water are still adequate for all.

Owen-Smith only recorded conflict among territorial males as a result of trespass. Richards (1972) saw two males fight while female and calf stood nearby. He also recorded a male trying to herd two females and in incidents where a female is present, it is likely that a clash between males will take place on a boundary.

As in the black rhinoceros, preliminary sparring may take the form of sideways swipes with the horn and in this way it is possible for horns to be split. However, Foster (1961) witnessed a remarkable incident that illustrated the ritualized nature of rhinoceroses' contests. "The fight had evidently been going on for some time, as there was an area of roughly 50 feet in diameter where the ground was trampled and the shrubs and trees broken. The two rhinos were battering at each other with their shoulders, like two enormous battering rams and not once while being watched did they use their horns.



Overall home range and core area of a female grass rhino superimposed upon a mosaic of male territories. The numbers of females recorded visiting two neighbouring territories are indicated; territory L was considered to offer optimum habitat. (After Owen-Smith, 1975.)



Chain displacement of territory holders. Male I displaces H. H becomes subsidiary (beta) male. After 12 weeks H moves to small territory. Sixteen weeks later H displaces X in neighbouring territory whereupon X displaces A as dominant (alpha) male. A remains as beta male for over one year. (After Owen-Smith, 1975.)

Their shoulders were bruised and appeared quite wet." Only in the most serious fighting are direct upwards stabs with the point of the horn employed. This suggests that the originally defensive components of fighting have been isolated from the aggressive one of direct thrusting and ritualized into a less dangerous fencing contest. Defeated bulls are not driven away but they adopt subordinate gestures to the victor; they stop spraying urine and gradually scatter their dung less as they progressively reduce the intensity of their foot wiping. They are also precluded from accompanying females and Owen-Smith (1975) recorded only 8% of all sightings whereas 39% of the alpha or dominant bull sightings were in the company of females. Owen-Smith also noted a chain displacement of territorial males resulting from the ingress of a single bull. The new owner was never observed to rise from the rank of subsidiary male within the same territory but such males can move into a neighbouring territory and displace an alpha male there. They immediately assume all the behaviour of a dominant animal, tending females, confronting other males, spraying boundaries and scattering dung. Boundaries are sometimes altered but are commonly inherited intact by the new tenant. Even more significant is the observance of territorial limits by the subsidiary males which have played no part in the establishment of these boundaries. Presumably the risk of unnecessary challenges are avoided in this way. The displaced bull ceases to spray urine and gradually stops scattering dung. Territories can be taken over after fights in which one or both contestants are wounded or there may be no evidence of a fight at all.

It is possible that outbreaks of fighting that have been observed in West Nile were the product of a similar upset in the territorial system. But the social life of grass rhinos has not yet been studied in East Africa. Although there are occasional fatalities from fighting, the slow breeding and maturation of this species is obviously related to a very low rate of natural mortality. Shortage of water has never been a problem on the banks of the Nile, yet the density of population has never even begun to approach the numbers reached in contemporary Zululand.

Young are born at intervals of two or three years and females in Zululand do not give birth until they are six-and-a-half to seven years old (Owen-Smith, 1975).

A female only elicits interest from the male when she is in oestrus, a condition she advertises by repeated sprayings of urine samples. A female may come into oestrus between six and eight months after giving birth, but Owen-Smith has suggested that a flush of green grass after a dry period may trigger oestrus and encourage the observable mating peaks seen in this species (October—December in South Africa and February—June in West Nile). A birth peak between July and November has been noted in Uganda.

Courtship is prolonged and Owen-Smith saw couples consorting together for 5—20 days. The male is usually cautious but persistent in his approaches to the female, which tends to threaten him at first, as does her calf. A territorial male tries to keep an oestrous female within his territory by heading her off and blocking her way, meanwhile uttering peculiar panting or hic-throbbing calls or actively chasing her back from a boundary with loud wails or squeals. He scrapes, urine-sprays and wipes his horn repeatedly (Owen-Smith, 1975). After 15—20 hours of persistent attendance the male's closer approach is tolerated and he lays his head along her back. Once the female stands still and curls her tail, the male may mount and copulation can last up to half an hour. That the whole affair places considerable demands upon the male was shown at Whipsnade Park Zoo when a copulating male had a heart attack and fell so heavily upon the female that she broke her back.

After a gestation of sixteen months the female chases off her previous offspring and gives birth well away from other rhinoceroses. Although the newborn rhino can stand within an hour, the mother remains in a secluded spot for a few days with the rather shaky youngster keeping very close. After

a few weeks they may join up with other rhinos and the young one starts grazing at two months. However, suckling is maintained for over a year, with the young one whining for its drink and taking its fill in two or three minutes.

A curious difference between *Ceratotherium* and *Diceros* is the tendency for calves of the former to take the lead. Even in flight the female appears to follow the direction taken by the young one.

Calves are often alert and curious but never leave their mothers out of reach. While it lasts this relationship is close and enduring but the necessity for a close companion is not lost when the juvenile is rejected. The subsequent rapid link-up of adolescents or unattached females suggests a continuing need by the immature for companionship.

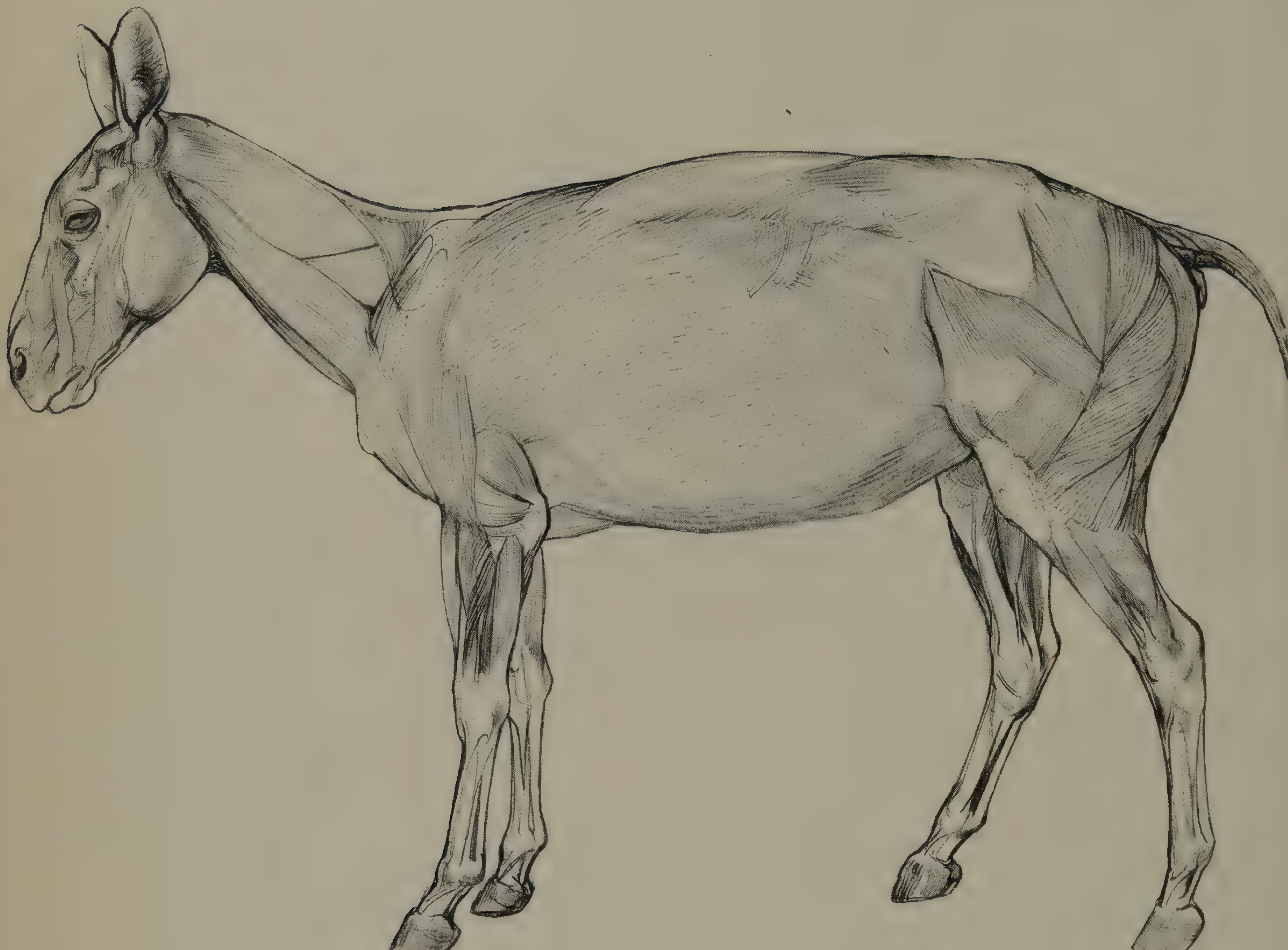
Until recently this species has been rare in zoos but they have proved to be almost ideal zoo animals, easy to feed and maintain in good health. They breed well in captivity and are generally tame and tractable; they can also be controlled by means of tranquillizing drugs.

A female has been recorded still bearing calves at 36 years old (Player and Feely, 1960) and total life expectancy is probably in the region of 40—50 years.

The vicissitudes of the Uganda population have been patchily chronicled in the annual reports of the Uganda Game Department. In 1924 an article was published in the Bulletin of the Zoological Society of New York which focused conservationists' attention on the status of the white rhinoceros. Largely as a result of this article, protective legislation and a summary census were attempted. Quantities of horns were on sale at this time and there are official records of some 182 horns from animals killed between 1923 and 1928. In the latter year a marked diminution in numbers and a total estimate of 133 Uganda rhinos was suggested (UGR, 1928). Over the next 20 years casualties were rare and the rhinos were almost unmolested; by about 1950 a healthy population of approximately 500 rhinos were scattered throughout the uncultivated areas of West Nile. At about this time the price of rhino horn rose, so over the next ten years poaching was very heavy and the rhinos were killed out in all their gazetted sanctuaries. By 1963 the sum total of Uganda rhinos was believed to number 71 (Hayes, 1964). Between 1961 and 1964, fifteen rhinos were darted and moved to Murchison Falls National Park and their last stronghold at Inde (Ajai's reserve) was gazetted as a rhino sanctuary. Since then poaching has continued on a reduced scale but a virtually domesticated rhino (nick-named Obongi and pictured in this profile) was killed within the national park.

Throughout this century and probably for several hundred years grass rhinos have lived in proximity with people. In the wake of local shifts or fluctuations in human settlement the rhinos have benefited, like the kob, from the clearings that surround old villages and the swards that form on abandoned fields. No conservation measures for the grass rhino can be successful without the support of the local people of West Nile. Unscrupulous and predominantly foreign middlemen offering to buy horns have been the opponents of the Uganda Game Department (and, in recent years, of a dedicated rhino warden, Dr Ted Williams of Kuluva Hospital). It is not only penalties that have encouraged the people to maintain their traditional

tolerance of these animals. In 1972 there were 120 rhinos in Ajai's Reserve; by early 1978 they had been reduced to 80. About 25 animals are now living in the Kabalega National Park.



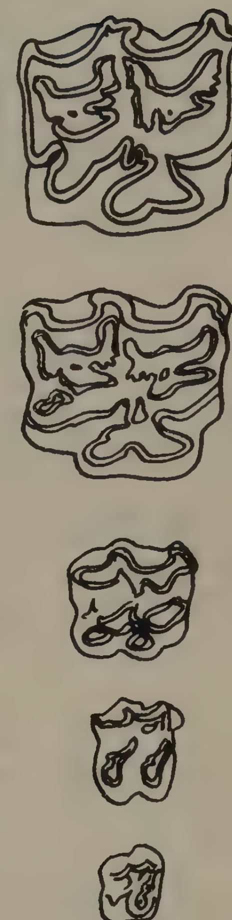
Equus quagga

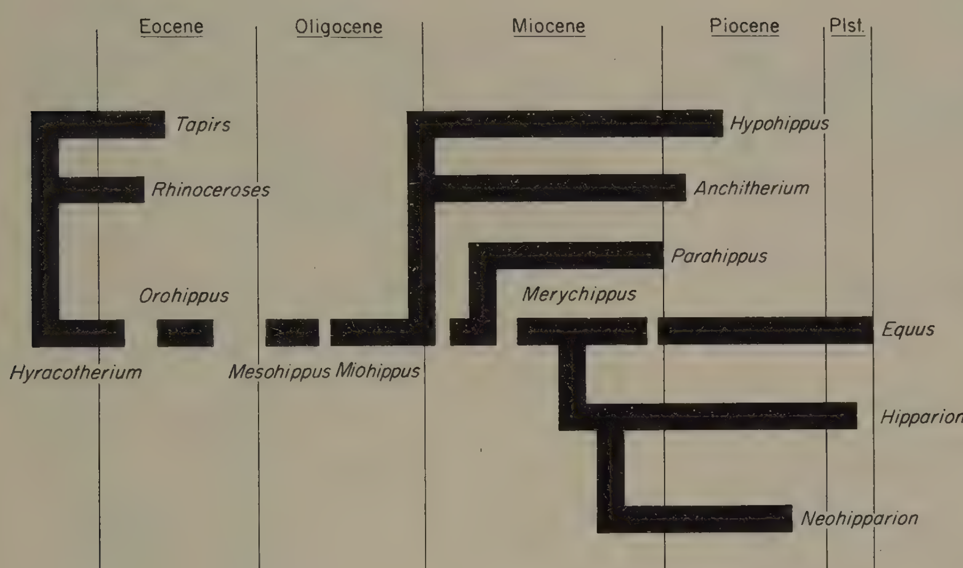
Equids, Horses

EQUIDAE

The evolution of horses is not an African story. *Hipparion* invaded Africa in the middle and *Equus* at the end of the Pliocene, arriving as highly evolved grazers that were able to compete with and in some cases perhaps displace indigenous ungulates.

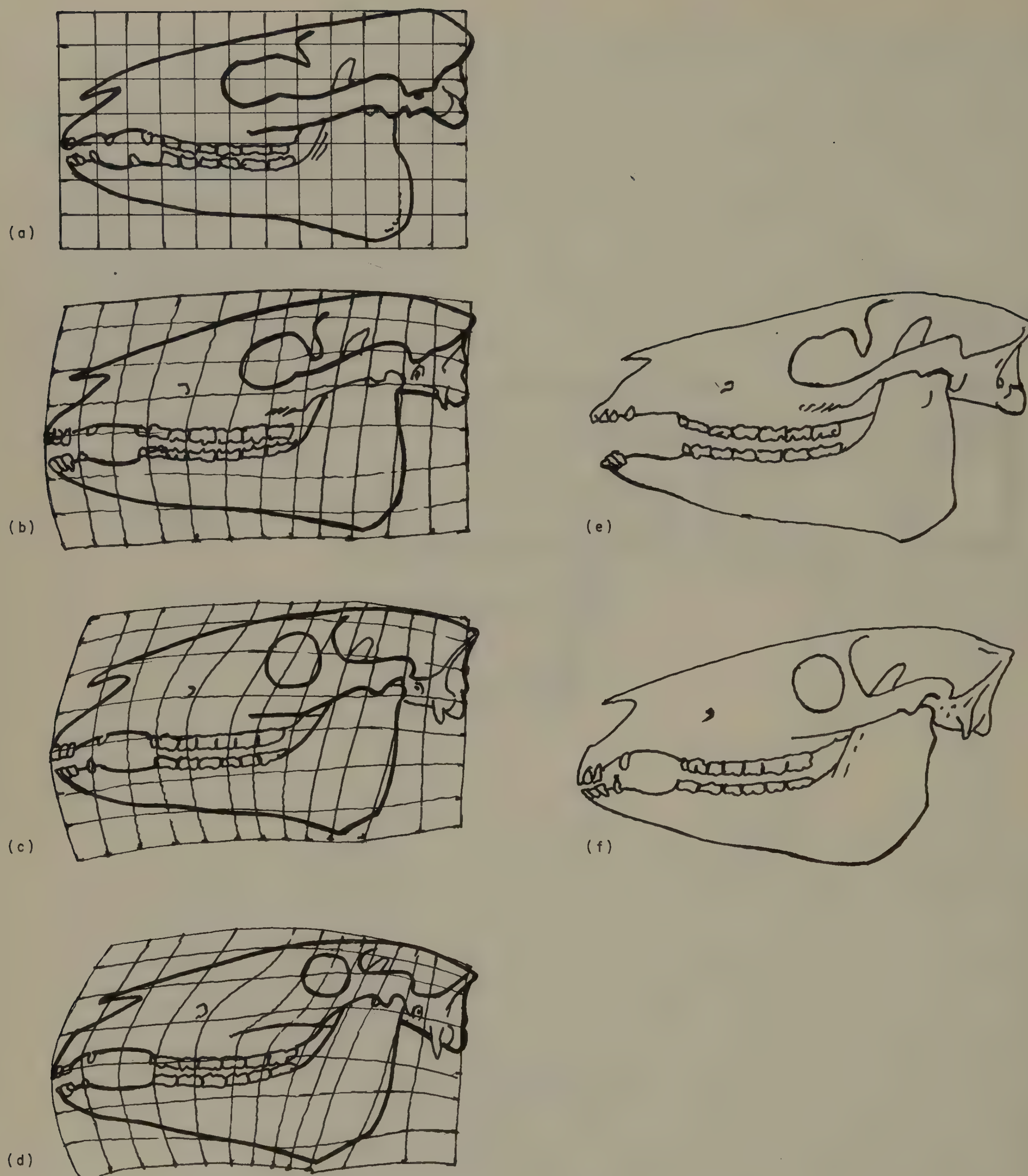
The equid evolution and radiation in America can be compared with that of artiodactyls because to some extent theirs was an earlier but parallel attempt to fill the herbivore niche. The earliest equid, *Hyracotherium* (formerly known as *Eohippus* or "dawn horse") was comparable with a tragulid. The animals were close to the stem of other perissodactyl types and were widely distributed in North America and Eurasia; they probably anticipated chevrotains in their occupation of a forest or swamp forest niche and are likely to have had a mixed but predominantly herbivorous diet.





Subsequent fossils are exclusively North American until the Miocene when advanced equids began to invade other continents. *Orohippus* and a specialized offshoot *Epiphippus* appeared late in the American Eocene. In the early Oligocene, *Mesohippus* and then the larger *Miohippus* continued the trend towards a more exclusively herbivorous diet. A diastema developed between the incisors (which became specialized for plucking) and the cheek teeth became more uniform and suited to grinding plant material. *Miohippus* and the later browsing equids resembled duikers in body build and they probably filled a similar niche. These browsers varied very greatly in size from the diminutive *Archaeohippus* to the gigantic *Megahippus*. One type, *Anchitherium*, seems to have been a particularly successful browser and persisted into the Pliocene in China.

In America, Miocene equids, *Parahippus* and *Merychippus* show adaptations that suggest tougher vegetation in their diet and harder soils underfoot. Teeth acquired a more complicated and deeper cusp pattern and cement appeared. Muzzles were elongated and limbs were longer and more slender. Changes in the proportions of the lower limbs were achieved by the retreat of side toes so that only the centre toes and their cylindrical metatarsals and metacarpals were functional.


(a)
(b)
(c)
(d)
(e)
(f)

These improvements in gait and dentition clearly allowed *Merychippus* to enter a new niche, that of a mobile and fleet footed grazer in more open habitats.

The Pliocene saw a new radiation of equids, the most successful of which was *Hipparion*, which invaded Eurasia and Africa, surviving in Africa until the mid-Pleistocene.

Comparisons of the skulls of equids from *Parahippus* to the modern horse show that the jaws deepened as the crowns lengthened, the brain enlarged, the distaema increased, the nasal area declined in relative importance and overall size increased (in the standardized figures opposite this is implied by the relatively smaller eye socket).

It is possible that *Equus* first emerged during the Miocene (Quinn, 1955) but the genus remained confined to North America until the mid-Pliocene.

Hopwood (1937a) concluded that horse-like and zebrine lineages could be recognized in the early Pleistocene, and MacGrew (1944) thought that the latter evolved in North America while a primary radiation of *Equus* might have led to the development of caballine horses in Eurasia which, with the onset of cold conditions, invaded North America and displaced the zebrine, *E. simplicidens*, which had been abundant in Texas and New Mexico in the later Pliocene.

The geography of the *Equus* radiation is still far from clear and it involves fragmentary fossils from four continents. Their ecological radiation is discussed in the next profile.

Opposite:
(a) *Hyracotherium*;
(b) *Equus*;
(b) and (c) Two intermediate skulls constructed on co-ordinate transformations (from D'Arcy W. Thompson, 1917);
(e) *Mesohippus* for comparison with hypothetical skull (b);
(f) *Merychippus* (*Protohippus*) for comparison with (c).

Horses, Zebras, Asses
Equus

Species

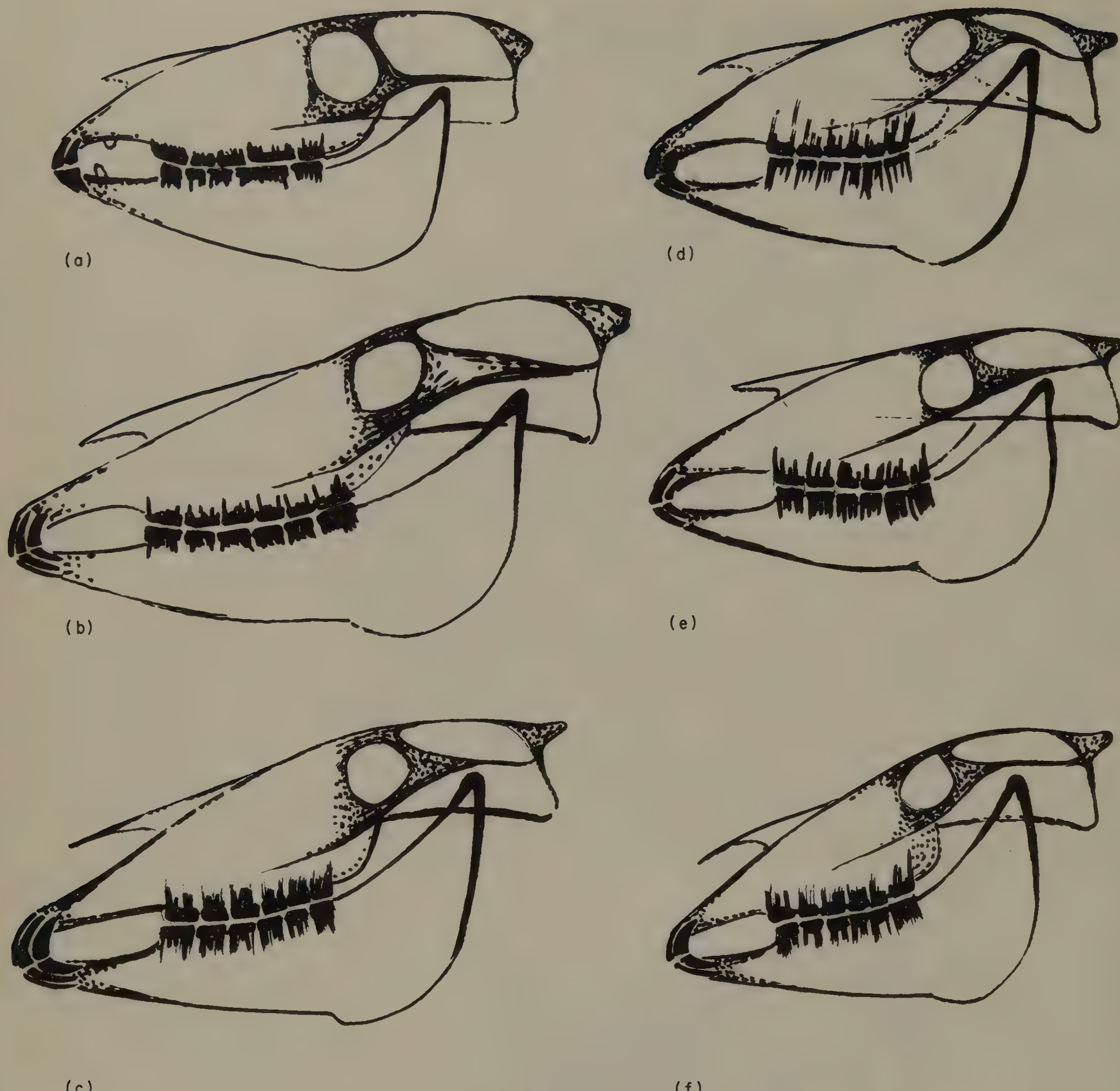
Equus grevyi
Equus quagga
Equus asinus (domestic and feral)
Equus caballus (domestic)

When grass first became widespread during the Miocene only a limited number of mammalian groups was able to adapt to this difficult food and those browsing herbivores that had already modified their digestion and dentition and were reasonably agile would have been at an advantage.

The herbivores that were available differed from continent to continent, in South America it was the notoungulates, in Australia it was marsupial kangaroos, in Eurasia and Africa it was artiodactyls and in North America the equids had a headstart in adapting to grassland.

In the end it was the stomach that counted. The greatest digestive efficiency developed in the ruminants, which store, sift, rechew and ferment vegetable particles so that metabolic elements are released at an early stage of digestion, thus allowing a more complete assimilation of nutrients.

Perissodactyls, in common with elephants, also break down cellulose by fermentation but they only chew their food once and assimilation begins after food has left the stomach and passed through the caecum. The dung of these animals betrays that plant material is less completely broken down. In spite of this equines are rather successful. One of the reasons is that they tolerate a wide range of grasses in their diet and are able to consume them at any stage of growth as long as the grass can be had in adequate quantities.



Diagrams of equid skulls indicating major functional zones. Differing proportions of these zones can be appreciated in primitive equids (a) and (b) and modern forms.

(a) *Merychippus republicans*;
(b) *Pliohippus perix*;
(c) *Equus grevyi*;
(d) *Equus quagga*;
(e) *Equus caballus*;
(f) *Equus asinus*.

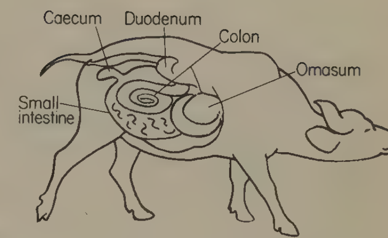
Opposite page:
Left: *Equus sanmeniensis*—Late Pleistocene, (China) (after Teihard and Piveteau).
Right: *Equus grevyi*.

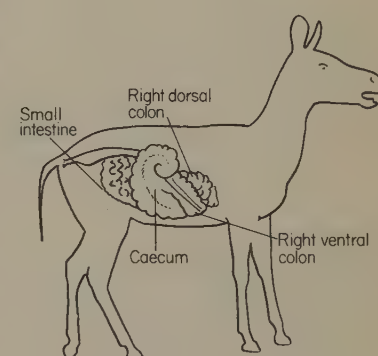
They have a simple stomach and food passes through their digestive system about twice as fast as in the average bovid (Alexander, 1952). On the same pasture they eat about twice as much as a comparable ruminant, which compensates for their inferior assimilation of protein (Glover and Duthie, 1958).

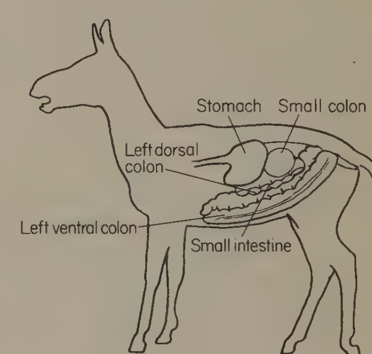
The food's speed of passage through the system is about 48 h in a horse and 70—90 h in bovines. The actual rate of breakdown in a rumen and in a horse's caecum is much the same and both the biochemistry and microbial taxa are similar. The major reason for a horse having about 70% of the digestive efficiency of a ruminant is that the cellulose remains in the fermentation chamber for a shorter time. Although the caecum and colon have been greatly enlarged and must provide an adequate surface area for absorbing nutrients the small intestine of a horse is relatively short. The digestive tract (with contents) represents only 15% of the body weight in horses compared with 40% in a bovine. These differences in weight distribution influence body architecture quite fundamentally and there must be trade-offs in relative efficiency that give different types of advantage to both these herbivore models.

The quantity of grass must also compensate to some extent for its poor nutritional value. Equines can survive in dry and barren areas on graze that is often tough and unpalatable to most bovids. The requirement for bulk is correlated with social habits that do not restrict movement; since ruminants need less of the available resources to sustain themselves and need graze only half as long, the depletion of a shared range will hit the equine first and they seem to have evolved strategies that avoid direct competition in such situations. In any event, equines are generally the first to move out of an overgrazed area, and most species are relatively nomadic.

It is very likely that *Equus* evolved most of these characteristics long before its arrival in Africa. Indeed the living species do not differ very greatly in their dental and cranial anatomy from fossils of the period when equids first expanded into Africa and they represent a distinct ecological array. By the beginning of the Pleistocene *E. plicatus* was present in southern Africa and *E. sanmeniensis* in China and both are sufficiently similar to *E. grevyi* to be possible chronospecies. Smaller equines with cranial resemblances to *E. quagga* have been found in early Pleistocene Asia (*E. sivalensis*), and the mid-Pliocene *E. sellardsi* in North America.



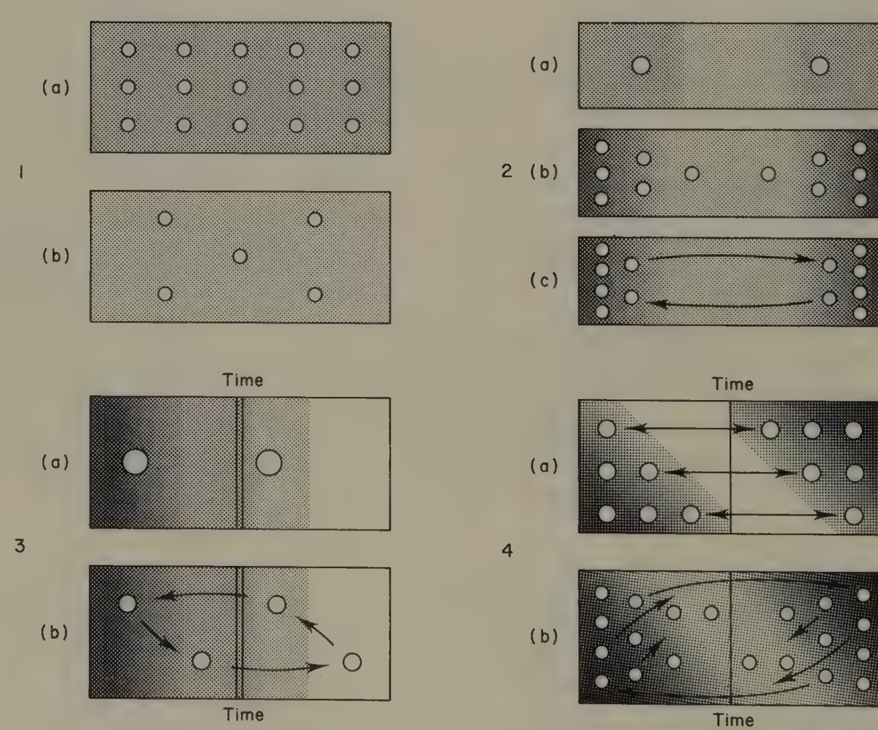




There is now considerable evidence that zebras, which have a number of conservative cranial features, first differentiated in North America (MacGrew, 1944; Quinn, 1955; Azzaroli, 1966).

Quinn (1955, 1957) has allocated teeth from allegedly Miocene sites in North America to distinct zebrine, asinine and caballine stocks, Azzaroli has suggested that the *E. grevyi* or "Dolichohippus" lineage is close to the ancestry of all the other living horses and that the smaller "hippotigrine" zebras derived from the more conservative "dolichohippine" lineage while asses and domestic horses might also have derived from early "hippotigrine" zebras. He considered that this differentiation into distinct lineages began before their migration out of North America.

Irrespective of their place of origin it is clear that the living equines represent an ecological array, the zebras occupying tropical grasslands, the asses deserts and the horses cooler grasslands in the northern hemisphere. As in other animals, these equines have accommodated their behaviour and their social systems to the disciplines of their environment and one way of examining the ecological niches of equines is to relate animal populations to the temporal and spatial distribution of their food.



1. Reliable and well distributed resources used by evenly spaced residents, density relative to level of resources (a) and (b).
2. Reliable but uneven resources used by (a) evenly spaced residents at low density; (b) unevenly spaced residents at a medium density; and (c) nomads at a medium overall density.
3. Unreliable resources used by (a) residents at a very low density; (b) nomads at a low overall density.
4. Temporally restricted resources used by (a) evenly spaced nomads at a medium overall density; and (b) variably spaced nomads at a high overall density.

When the resources of large ecosystems are relatively permanent and well distributed, animals can best use such habitats by being equally well distributed. Under stable conditions territorial behaviour can provide a mechanism that spaces a population out at a suitable density and this is a common strategy

in tropical forest communities. No equid is adapted to such conditions today but early equids were forest dwellers and may have resembled tapirs in being sedentary and solitary.

Where resources are unevenly distributed in space, resident animal populations must have social systems that are sufficiently plastic to accommodate to an equally uneven density or they will stabilize at a very low level. Alternatively they must become nomadic. If the carrying capacity of the range is subject to periodic changes the animal population is also likely to fluctuate. The deserts of Eurasia and North Africa pose some of these difficulties for wild asses. Where resources remain well distributed but there are broad ecological and seasonal gradients it may be possible for animal populations to maintain their density but they must become periodically nomadic and fixed territories become inappropriate. These were perhaps the characteristics of the great plains and valleys of the northern hemisphere where the wild horse, *E. caballus*, once flourished.

Finally, if an ecosystem has unevenly distributed resources in both time and space, animals can exploit the range most effectively by being nomadic and continually adjusting their own density to the nature of their resources. This puts considerable demands upon the social system; yet it is to precisely this situation that the common zebra is adapted. Great numbers will concentrate on local seasonal flushes and move together with or ahead of herds of various other herbivores. As the grass is consumed the zebras pass on to new pastures or scatter out into small family groups over much larger areas. They are both nomadic and socially versatile so that densities can accommodate to the vagaries of climate and grazing. How was this social mobility evolved and how does it relate to the other equids?

As primitive equids adapted to more open habitats they were likely to have become more social but the antisocial nature of solitary animals would not have been easily overcome. Indeed, a close examination of horse behaviour reveals that both sexes show signs of fundamental intolerance and that elaborate mechanisms may have been evolved to overcome this. In the earlier stages of their social evolution equines may have adapted to various forms of territorial behaviour. Two living species, the African ass and Grevy's zebra have territories that are the largest known for any herbivore (Klingel, 1972). The latter species resembles the common zebra in responding to fluctuating conditions of their range with changes of density and most of the animals are able to disperse or concentrate without inhibition, moving in small mother-young units, as individuals or in various temporary combinations. In some areas mating is monopolized by mature males after they have established residence and these stallions are not normally challenged by transients. Females are only warded by the territorial stallion for the period of their oestrus, so that all but the territorial males are free to seek out the best pastures.

When competition for mating rights is extra-territorial and open to all males, females can only be monopolized with an enormous expenditure of time and energy on the part of males and on this criterion a territorial system achieves greater economies. Klingel (1972) has recorded intense competition for oestrous females by non-territorial males of *E. grevyi* and he pointed out that reproduction is impaired and the female stressed.

In rich and relatively stable habitats this type of territorial system would have been efficient and would have represented an evolutionary advance on simple male–female or pair territories but with seasonal and spatial fluctuations in distribution of grass or water the retention of a territorial system becomes inefficient. Grevy's zebra stallions remain for half the year scattered across an empty dried out land and there is no doubt that in such circumstances the common zebra's wholly nomadic social system is superior. In many habitats the inability of Grevy's zebra to emancipate itself from territorialism probably rendered it inferior to more versatile equine competitors and it may help to explain the relic status of this zebra.

It is unwise to reconstruct the evolution of social behaviour by extrapolation from incompletely understood living species. Nevertheless, it is tempting to seek the origins of the common zebra's wholly nomadic social system in a territorial organization like that of Grevy's zebra. Territorialism could have been by-passed if there were populations of early zebras in which both sexes simultaneously became equally nomadic and this could be a simple explanation. The possibility should be considered that territorialism was a functional phase in equine evolution and that nomadism was consequent upon the development of a distinct class of non-territorial males. If this was so, Grevy's zebra provides an illustration of how the common zebra's social system might have evolved.

Reproductive efficiency in a territorial system generally requires that receptive females provide a strong stimulus and can be easily found and identified. When mating is free for all the expenditure of energy by competing males is enormous but mating opportunities are spread out more equitably because even the most active and dominant male can only win a very limited number of females. The most persistent male is the most likely to reproduce and in his persistence lies the potential for extending his association with the female.

In newly formed units of *E. zebra*, Joubert (1972a) found that the stallion actively avoids contact with other zebras but herds his female or family group very aggressively. Only when his dominance is unchallenged by the females in the group do his threats become very rare. Although he may provide a passive shield for persecuted members of the female hierarchy that then develops he plays little part in the social organization of the unit and is primarily concerned with intercepting other males that show an interest in the females of his unit.

Permanent attendance by a male reduces the need for over-advertisement of oestrus and this not only saves energy expended in male competition but a minor reduction in the conspicuousness of oestrus signals favours attendant males at the expense of territorials and undermines the function of the territories. Klingel (1967) has contrasted the very exaggerated oestrus behaviour of young *E. q. boehmi* with mature females which show no external signs of their oestrus and he has described the progression whereby males compete intensely for the period of a filly's first oestrus and then, oestrus by oestrus, other males are excluded as the filly's ties with a particular male become stronger.

If we imagine a situation in which there is increasing persistence in the association of females with non-territorial males and decreasing contact with territorials, a social system similar to that of Grevy's zebra could evolve into a non-territorial society in which each male attended one or more females and accompanied them in their movements between pastures. It is perhaps significant that mature females tend to initiate and lead movements in all equine societies.

It is possible that territorialism may reappear and that equine societies have some flexibility in this respect; Bruemmer (1967) has described feral horse stallions living on an island establishing territories. Nonetheless, horses, like common zebras are usually without territorial ties and the stallion defends his mobile family group rather than his mating rights in an area and this represents an advance in terms of ecological adaptation and perhaps in reproductive efficiency as well.

The overall size of a horse family's home range varies enormously and perhaps the area correlates closely with the year-round resources of the range. Feist (1971) estimated ranges of 2·400 hectares in Wyoming and he noted that stallions would drive their family bands away from another band or from stallions and would defend an area of about 100 m around their group. He concluded that the mutual intolerance of family stallions functions as a spacing mechanism. Wild jackasses are reported to be even more intolerant of one another.

The utility of spacing is clear in habitats with well distributed or dispersed resources but where these resources are locally or seasonally concentrated, male intolerance is not a favourable strategy and this may explain the striking difference between the behaviour of horse and zebra stallions.

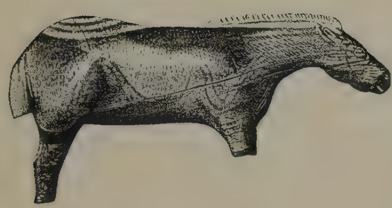
All equines will form bachelor groups but only zebra stallions tolerate the close proximity of other males. In Grevy's zebra, a territory holder will keep company with transient bachelors or, during the dry season, isolated stallions may pair up. Common zebras form dense aggregations on choice pastures in which numerous family stallions associate with one another as well as with other males.

In spite of the horse and the common zebra having similar family units, the socially dissimilar zebra species resemble one another in their ability to concentrate or disperse according to the vicissitudes of the environment. I believe that an explanation of this resemblance lies in the zebra's retention of certain conservative but adaptive features, chief of which is the possession of stripes.

Stripes could be an important mechanism counteracting mutual intolerance and, although males may be important mediators in the spatial dispersal of a population, the evolution of this device might have embraced all classes and both sexes in a common ancestral equid.

The presence of stripes on the legs and shoulders of wild horses, *Equus caballus przewalskii*, and similar vestiges on some species of ass are consistent with the idea that all modern equines derive from striped zebrine ancestors. Modern domestic horses sometimes have narrow stripes on the legs, shoulders, withers and rump and zebra-like markings appear on the forehead of horses from places as far apart as Norway and Afghanistan.

Darwin (1868) described a two-week-old colt he had bred.



Striped ivory horse from Lourdes. Palaeolithic.

"It had only a trace of the spinal stripe, with a few obscure transverse bars on the legs, but almost the whole body was marked with very narrow dark stripes, in most parts so obscure as to be visible only in certain lights, like the stripes which may be seen on black kittens. These stripes were distinct on the hind-quarters where they diverged from the spine and pointed a little forwards; many of them as they diverged became a little branched, exactly in the same manner as in some zebrine species. The stripes were plainest on the forehead between the ears, where they formed a set of pointed arches one under the other, decreasing in size downwards towards the muzzle; exactly similar marks may be seen on the forehead of the quagga and Burchell's zebra."

The paintings, rock engravings and carvings of Palaeolithic Europe also represent several species of wild horses including polymorphic types and extensive but variable areas of striping are often depicted in these images.

In the course of becoming social, many mammals (including most artiodactyls) have evolved complex social rituals which are expensive in terms of time and energy. If an equid must be mobile as well as needing twice the foraging area and twice the feeding time to compete with a bovid it gains obvious economies in time and energy if social behaviour can be abbreviated or simplified. A close look at all equid societies suggests that mares are fundamentally intolerant of one another (unlike most bovids) while the advertisement of an oestrous female reveals intense rivalry in the stallions of every species. It is just such anti-social traits that would have had to be suppressed or neutralized by equids during their socialization, an evolutionary process that was probably accelerated when they emerged into more open habitats.

Striped horses incised on bone. Southern Europe, Palaeolithic.

Every equine society has the mother and her offspring as the basic unit. The tightest bonds of all are between a mare and her foal. Both remain the closest companions until a new foal is born and even after this point the offspring's continuing attachment to its mother sometimes provides the nucleus for a larger and lasting family group.

An unweaned foal spends many hours sleeping or resting but it also seeks a playmate which, in the absence of another foal, may be the mother, which needing to graze most of the time in order to maintain her lactation, tries to ignore her foal's importunity. By the time a foal is two or three months old it may be spending more time with young companions than with the mother. The availability of other foals varies with the local density of animals and with the species of equines but, at this early stage, the foals discriminate in their choice of playmates preferring a foal of the opposite sex. Play between colts is also common but tends to be rough and to end in mock fighting. Play between fillies is much rarer and in spite of a general tendency for two or more mothers to be loosely associated, very intimate contact between females is generally avoided.

Sustained associations between mare units may be enforced by a stallion's herding activity, by extension of a single family or else by a very limited number of mares staying together spontaneously (Tyler, 1972; Klingel, 1969c; Joubert, 1972a).

Depending on the species, young males have a period of attachment to the mother's group, or else they join a bachelor group.

A measure of the indifference of adult females to one another is found in the infrequency with which they indulge in mutual grooming and it has long been recognized that no horse ever allows a strange or hostile animal to touch it, let alone groom it.

Grooming is generally mutual and establishes close contact between individuals. A typical sequence begins with sniffing at the noses and then nibbling at each others necks and shoulders and the bout is sometimes continued in a head-to-tail position with each animal grooming the other's rump and the root of its tail. This sequence is followed by zebras that have a stable relationship but they tend to interrupt or replace the nibbling action with token touches without opening the mouth, or they rest and rub their heads or chins on the partner. Foals nibble at the mothers' or playmates' legs in the course of various playful interactions. This is commonest with colts, among which grooming frequently precedes or is interspersed with playful fighting in which the legs and neck are nipped or bitten.

Like primates and many other mammals, equids seem to have relied on ritualized body-care to mediate the closest of their social contacts. In her study of New Forest ponies, Tyler (1972) remarked that grooming serves to reduce avoidance or fear responses in subordinates and so allows dominant animals to maintain social contact with those of lower status. She recorded a sharp rise in the frequency of grooming when horses were forced into close proximity in the shade of trees during high summer. Heckler (1971) found that grooming was restricted to members of a family group and each horse had only a limited number of grooming partners. He recorded a strong preference for the mane and withers (77·7%) with only 10·6% of the grooming focussing on the rump and tail base. Males nibble and lick the legs of females during courtship, but the legs are not normally groomed by adults. Feist (1971) found all combinations of grooming partners within a group, except for the stallion and foals and the activity appears to forge temporary bonds and to appease or resolve aggression.

In free-ranging ponies in the northern hemisphere there is an increase in the frequency of mutual grooming when winter coats are moulted in spring, and this primary function for grooming is obvious. In the tropics, moulting does not have the importance that it has in colder climates and short-haired tropical horses groom more as a social function than for body care. Why then is it not employed in the numerous casual interactions of zebras?

I believe zebras to have evolved a mechanism that allows the time-consuming gestures of grooming to be abbreviated and at the same time to make physical contacts between casual partners redundant with the added benefit that intolerance can be overcome as any conspecific, even a potential antagonist, can become an attractive temporary partner.

During rest periods, common zebra stallions or bachelors form partnerships or small clumps and frequently lay their heads on one another's rumps or shoulders, or lean and jostle against one another. These poses resemble mutual grooming both in gesture and in social context but they are seldom accompanied by nibbling. They also rub the sides of one another's faces in lieu of grooming and I have frequently observed zebras that have been separated from the family unit respond to the stallion's bray by running up to him to rub faces and, sometimes briefly leaning against him. These gestures

Equus grevyi

are commonest in subadult animals and they appear to be submissive. Token rubs or leans are also common gestures of submission by adult females towards the stallion. Another gesture deriving from grooming is champing of the lips or chewing motions which are common to all zebra species in situations where it seems to resolve tension. Joubert (1972a) recorded this gesture in dominant males of *E. zebra* to other dominants or to submissive males, in males to females and females to foals and he remarked that the motion may provoke a sensation from the vibrissae round the mouth. In this connexion it is interesting that foals of *E. grevyi* suck and tug at their mothers' exceptionally long oral vibrissae. Joubert also recorded *E. zebra* stallions of equal status rubbing their foreheads on one another's rumps.

Head rubbing has the motor pattern of grooming and observation of foals suggests that it derives directly from grooming in the ontogenetic development of an animal (although it is possible that sucking behaviour has an influence). As I stated earlier young zebras of both species nibble their mothers much more frequently than the mothers do them. As the foal gets older, it tends to rub rather than groom. When a partner approaches it also nods in a manner suggestive of grooming *in vacuo* and this may be reciprocal. Nodding may be maintained while the two animals stand in close proximity but out of physical contact. This may be significant because adults, particularly of Grevy's zebra, have retained the pattern of coming to a halt parallel to their partner but they usually dispense with grooming and with the need to touch one another. Even the gesture of nodding is generally absent, suggesting that these animals have emancipated themselves from the need to groom.

I will now consider the relevance of these observations to the evolution of stripes and hope to show how exclusive individual bonds forged by tactile contact in an ancestral equid might have been replaced in the evolutionary development of zebras by a visually-based bonding system. Since a theoretical advantage of such a system would be greater social mobility, I have been especially interested in Grevy's zebra, which is the most evenly striped and which has the least exclusive social relationships.

Opposite page: Accommodation of horizontal leg-stripe to vertical body-stripe system in (a) *Equus grevyi*, (b) *Equus zebra*, (c) Hypothetical ancestral equine, (d) Hybrid *Equus grevyi* and *Equus zebra*.

Many mammals have special patterns restricted to target areas of the body. For example, *Hyaena hyaena* has a black throat which is presented for grooming, pale shoulders and rump, which are bitten during fights and long striped legs which are folded out of the way during any hostile encounter. It is possible that stripes developed on the zebras' legs for reasons similar to those of the hyaena, certainly their fighting techniques have something in common (see Volume IIIA). Likewise the okapi's rump stripes may have social functions comparable to those of zebras (see p. 339). Since Somali asses and Przewalski horses generally have plain bodies and striped legs while some Magdalenian horses and the Cape quagga had striped forequarters and plain legs, similar patterns on dissimilar sites could serve different purposes.

It is common for a preferred grooming area to be differentiated in the texture, colour or pattern of the fur. When an equid raises its head, the skin at the base of the neck wrinkles. In a short-maned, short-haired horse, this folding of the skin is perceptible to the eye and to the touch. Because this is also a target area for grooming, it is conceivable that fine barring on the withers might have originated as an enhancement or mimicry of this physical characteristic to guide a partner to the preferred site for nibbling. Whatever the origins of stripes it can be predicted that small nodding movements of the groomer's head and movements of the eye close to a narrowly barred black and white area should have a definite neurophysiological effect in the groomer's brain. Nerve cells programmed to particular spatial frequencies have been discovered in the visual system of animals and Mollon (1974) has remarked that this system could be regarded as several sense organs rather than one, experiments on animals having shown that the visual cortex contains individual nerve cells that respond only to edges of a particular orientation or only to movement in a particular direction, or only to stimuli at a given distance from the eyes.

Zebras have evolved a pattern that seems to exploit some of the primary responses of visual neurones to sharp edges, orientation, spatial frequency and, since viewer and viewed are seldom altogether still, to the "flicker-effect" or of alternating black and white linear stimuli combined with movement.

There is no way of knowing how barring affects zebras but there have been numerous experiments on the effects on human perception of black and white bar patterns of differing frequency and orientation (Gibson, 1966; Mollon, 1974). Because the zebra foal begins grooming at a very early age and tends slowly to reduce this activity as it grows up, it is possible that the stripes exert an influence on the zebra's behaviour through a process of conditioning, in which case the response to the stripes would not be innate. In any event it is very likely that the barred surroundings of the parental herd and more specifically of the mother might have a powerful conditioning effect on the zebra foal by associating an intimate and rewarding social situation with a strong visual sensation.

If the stripes facilitate socialisation, this could find some expression in the spacing of individual zebras. In order to demonstrate that horses and zebras are different in this respect, I have compared the spacing of nearest neighbours in groups of Grevy's and common zebras and English horses, correlating distance with orientation and activity. I have been unable to record any significant difference between the three species when they are grazing or


(a)


(b)


(c)

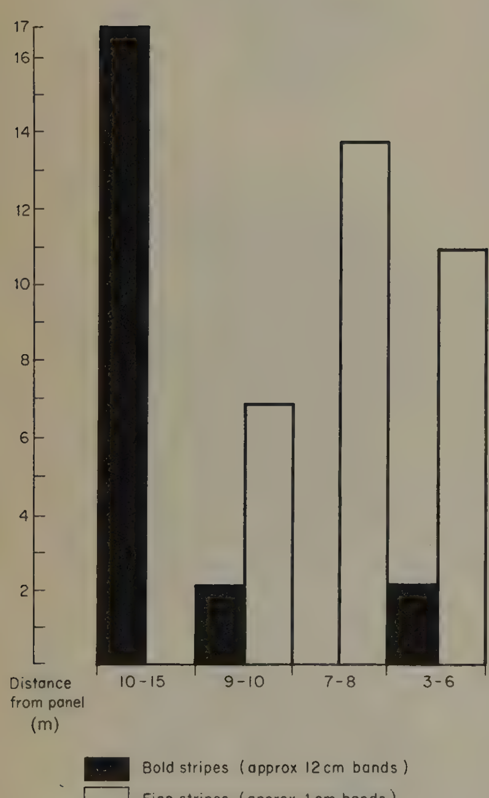

(d)

walking in line. All equids tend to walk in single file if they are undisturbed and bunch together tightly if they are chased or attacked. This may originate in the infantile pattern, when a foal normally follows close on its mother's heels but comes up against the side of her body at the slightest alarm. Therefore, when an equid is calmly walking along its nearest neighbour is likely to be directly in front or behind.

Slight differences in the group structure are apparent when the animals are galloping together in a tight bunch, but the most revealing differences between species are in the orientation and distance of one animal to another when it comes to a halt. Domestic horses tend to approach from any direction, sometimes stopping to look at one another before they approach nose to nose. Variations in both coat patterns and whinnies allow the identification of individuals. Distances and orientation are very variable. This is not so for the less xenophobic zebras, among which there is great consistency in the orientation and distance of one zebra's halting near another. Zebras tend to come to a halt parallel with one another; when they face the same direction, the animal stopping beside another is very often slightly ahead or behind. In Grevy's zebra I found that 79% of all observed halts were parallel and of these 81% were within two metres of the nearest neighbour: 70% of the common zebra halted parallel but the average distance between neighbours was appreciably wider. For the domestic horse I recorded 34% halting parallel to their nearest neighbour and there was little consistency in the distance.

The shorter distance between individuals of *E. grevyi* relative to *E. quagga* might have some connexion with the narrower frequency of their stripes and it is possible that the visual receptors might be more sensitive to a particular range of band frequencies, which could help to govern the spacing of individuals.

To test the sensitivity of Grevy's zebra to stripe frequency I accustomed nine captives (by kind permission of their owner, Mr J. Knowles) to two rectangular panels on which vertical bars were painted. One set of stripes was wider than any found on a real zebra: those on the other panel were very narrow and numerous. The panels were erected at the zebra's eye level round a tree trunk growing near the centre of an enclosure and they faced opposite directions. Each was about 3 sq m in area and dominated the visual field of a zebra in the pen. The animal was free to stand anywhere up to 10 or 15 m away. Single animals were released into this pen for an hour at a time and their orientation and distance in relation to the panels, as well as their activity was recorded at intervals of one minute. An animal ignored the panels if it was distracted or disturbed and it often paced the peripheries of the enclosure but it would sometimes stop and come to rest in view of one or other of the panels. The reactions varied from staring with pricked ears and occasional nodding of the head to avoidance gestures, particularly when suddenly coming into full view at close quarters. There were also individual differences; for example, when a nursing mare that was less familiar with the panels was led into the pen with her foal, she tended to draw her ears back whenever she turned inwards and once directed a typical threat at the finely striped panel, backing towards it and giving an aggressive buck. Two foals which accompanied their mother each showed more interest in this panel than



Number of times in which zebra stood facing or lateral to panel of stripes.

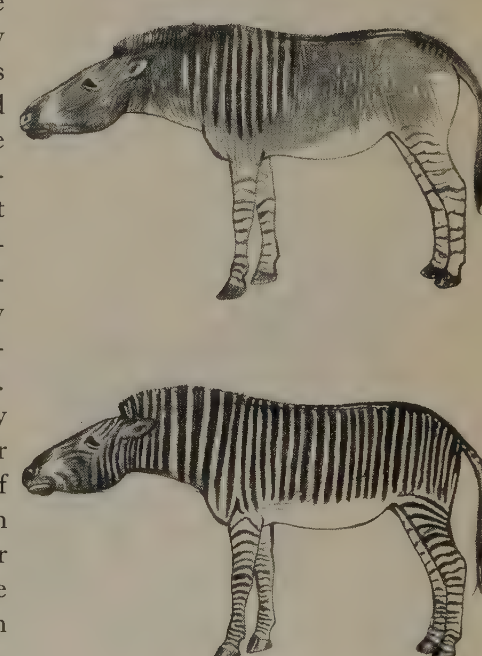
the large striped one. Other individuals were apparently indifferent, but when the distances of animals from the panels were totalled a marked tendency for animals to be closer to the very narrow stripes and further from the very broad ones was revealed (see margin chart, opposite).

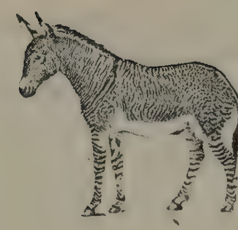
This finding might be open to more than one interpretation and more sophisticated experiments might lead to more conclusive results. Nonetheless, the zebras' behaviour accords with my observations in the field in suggesting that spacing between nearest neighbours may be influenced by the frequency of black and white stripes. One further observation emerged from my comparisons of horses with wild and captive Grevy's zebras. During their nomadic existence in the subdesert any individual of *E. grevyi* can link up with another and there is scarcely a trace of the exclusiveness that is manifested in the limited number of grooming relationships among domestic horses. However, within small groups of zebras confined permanently together, preferences for particular partners do develop and Rainy (personal communication) has observed grooming among wild stallions that had paired up after having been deserted by the nomadic herds. Grooming among these partners is much more frequent than among casual acquaintances, which tends to confirm the connexion between physical grooming and the maintenance of close bonds between individuals. These bonds are maintained by frequent grooming within the enlarged social units of the common zebra but actual physical contact is avoided in the numerous interactions with other units. It is in the potentially disruptive meetings of males that ritualized nodding, rubbing or mere standing, can be seen to perform a particularly vital social role.

Inherently exclusive, mutual grooming is an inappropriate social adhesive in crowded situations where sustained relationships are difficult or disadvantageous. Besides, in highly competitive poly-specific situations it is also time and energy consuming. So long as units are small and relatively stable, social cohesion is well served by grooming as a mechanism but the exclusive nature of grooming makes it an obstacle to the easy, temporary coming together of unrelated animals. If, as I have suggested, equine stripes originally evolved as foci for grooming behaviour, the ancestral zebras would have associated almost from birth, the tactile stimulus of grooming with the visually based neurophysiological stimulus induced by barring. The attractions of grooming became transferred by visual association to the mere sight of a striped shoulder, haunch or leg, so that the less discriminative relationships were facilitated. If grooming was the principal mechanism counteracting mutual avoidance its social function would not only have been greatly extended in scope but it would have been qualitatively changed by association with a pattern that made other conspecifics indiscriminately attractive.

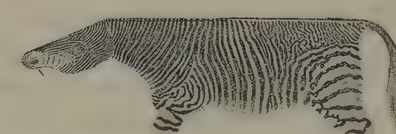
Once the stripes actually played a positive role in promoting sociability they would have lost their subsidiary function as foci for grooming and their effectiveness would have been diminished by being limited to certain parts of the body so that a more efficient use of the mechanism required the extension of striping to embrace the whole animal. Since the stripes may have their optimal effect when individuals are at a specific distance from each other, the stripes might have acquired the secondary function of helping, in certain circumstances, to space zebras.

Hypothetical ancestral equids showing extension of shoulder and leg striping.





Coat patterns in above left: *Equus quagga burchelli* × *Equus asinus hemionus* hybrid.
Above centre and right: two *Equus zebra* × *Equus asinus* hybrids.



Right: *Equus quagga boehmi* × *Equus caballus* hybrid.
Left: *Equus grevyi* × *Equus zebra* hybrid.

Equus quagga quagga × *Equus caballus* hybrid.

Equus grevyi × *Equus caballus* hybrid.

It seems very likely that horses derived from a narrow-striped zebra because this is the pattern found on morphs such as the one described by Darwin in 1868 and because hybrids between horses and common zebras always have narrow stripes completely unlike those of their parent, likewise common zebra-ass hybrids usually have many indistinct stripes on the neck and body and spots on the hind quarters. An interesting hybrid bred by Lord Morton in about 1820 came from a Cape quagga stallion crossed with an Arab mare, the offspring had three shoulder stripes and banding round the knees and hocks in spite of both parents having unstriped legs.

There is no evidence for wild horses ever entering Africa. Domesticated horses arrived in Egypt in 1600 B.C. and a horse represented in a rock painting at Ennedi in the Sahara probably post-dates their arrival.

There is much contention over the ancestry of caballine horses in North America; *E. scotti* and *E. laurentius* are only from the Upper Pleistocene. Hopwood (1936) concluded that caballine horses were distinct by the early Pleistocene but Quinn (1955) has claimed to recognize the lineage as early as the Miocene. In Europe, *E. simonescui* from the lower Pleistocene in Rumania represents an early caballine horse (Groves, 1974) while Azzaroli (1966) holds that the mid-Pleistocene Mosbach horse from Germany is unequivocally ancestral to the domestic horse.

Equus caballus became dominant in northern latitudes with the onset of the glacials and small types, often called *E. ferus*, were widespread in tundras of Siberia, Alaska and northern Europe. Apart from *E. przewalskii* the last few score of this type of horse may still exist on Exmoor in south-western England. Zebrine horses disappeared from North America with the onset of the glacials (MacGrew, 1944) but probably continued to survive in southern Eurasia up to 100,000 years ago (in *E. valeriani* from Uzbekistan which might be synonymous with *E. grevyi*).

Instead of a tropical situation with concentrated resources and many other physiologically superior herbivores in continuous competition, the cold north offered very abundant seasonal grazing over a vast area. These were only available to the few specially adapted species that could move between distant pastures and survive the cold winter on coarse diets. Deserts presented similar rigours but horses and asses have proved to be well adapted to live in these demanding habitats. However there is no evidence for their having congregated in the numbers zebras do. The refined social functions that I have proposed for striping would have become redundant for dispersed units in harsher environments, within simpler ecological communities. Although he was unable to propose a function for stripes, Ewart (1899) remarked that stripes were presumably useful to equids living in wide, fertile, richly populated plains, while they may have been useless for horses living in remote desert regions. It is interesting that Palaeolithic cave paintings in Europe depict a variety of patterns on horses, many of which show bold striping on the neck and shoulders or circular spotting of the body suggestive of a wide range of individual variation. Without this evidence for polymorphism in wild horses before him Ewart (1899) remarked on piebald and other patterns. "The pigment which formerly produced stripes has in recent times been as it were left uncontrolled with the result that it frequently gives rise to ever-varying and quite meaningless dappling or to large equally meaningless blotches." Put in the perspective of this discussion it is possible that as the function of stripes became redundant, selection against various aberrant patterns ceased to operate. This can be illustrated by comparing the patterns of aberrant wild zebras with those represented in cave art. In some situations polymorphism might have had the function of assisting the recognition of individuals. It is also interesting that a decline in the area of stripes as well as a high degree of polymorphism can be observed in the most southerly population of *E. quagga*, the extinct Cape quagga. Although only 17 mounted skins are known to exist (Harper, 1945) plus a few pictures, the range of variation was evidently far greater than that of living zebra populations (colour plate). The Cape quagga shared the highly differentiated Karroo biotope with a fauna that was distinctive but impoverished when compared with its tropical counterparts. The skull of *E. quagga quagga* is distinctive and Cabrera (1936) remarked on its resemblance with that of a horse with straight profile and concave diastema and similar cephalic indices. It is possible, therefore, that the Cape quagga was an incipient species recapitulating in miniature the evolution of the horse, which may have derived from a similar zebrine stock in the northern hemisphere.

Finally, it should not go without remark that irrespective of their exact functions, crisp linear patterns are impossible to maintain in a thick winter fleece that is moulted every year and both horses and Cape quaggas had thicker winter coats than tropical zebras.

Considering the rarity of aberrant patterns in zebras there must be remarkably strong selection in favour of a clearly defined and repetitive stripe system with relatively narrow ranges of variation in spacing. This genetic consistency in three very distinct species implies that the function of stripes must be of central importance in the biology of zebras.

Polymorphism in equines

FIRST COLUMN

Equus quagga boehmi (from skins and photographs of living animals).

SECOND COLUMN

Equus quagga quagga (from skins, photographs of living animals and contemporary paintings and descriptions).

THIRD COLUMN

Equus caballus (from Palaeolithic rock paintings in Lascaux, Dordogne, France).

Distribution of subcutaneous yellow fat and dermal muscle on flanks and rump of common zebra. Strips are under black stripes only suggesting fat may act as a heat umbrella.

Various mechanical explanations have been proposed for zebra stripes, for example that certain growth processes or conditions of strain were distributed over the skin of early embryos or that the patterns follow imaginary embryonic folds. Portman (1952) pointed out that however much the zebras' designs may resemble patterns that represent time sequences as the structure grows (such as snail shells or bird feathers), their mode of formation is quite different, being directed by very complicated systems of hereditary factors.

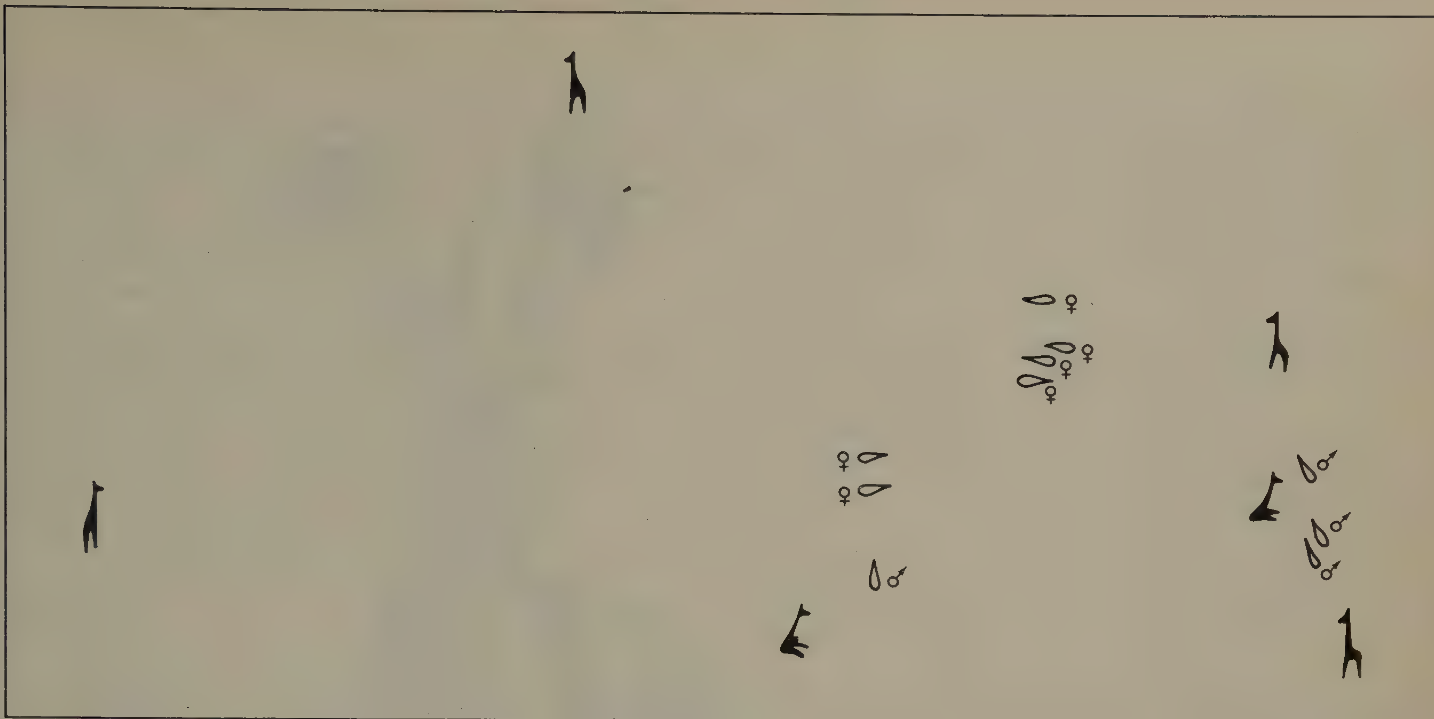
A simple mechanism for pattern formation has also been suggested to explain the different spacing of stripes in the three species of zebra; Bard (1977) thought that the laying down of equidistant stripes at different points in embryogenesis could produce the appropriate adult pattern. He suggested that the spacing is determined during the third week in *E. quagga*, fourth week in *E. zebra* and fifth week in *E. grevyi*.

Zebras play a dynamic role in the tropical grassland ecosystem. In his pioneer work on grazing successions, Vesey-FitzGerald (1960) invoked the common zebra as one of the precursors that improve the range for short grass grazers. Even species with a tolerance for long grass, such as buffalo, kongoni and topi, sometimes benefit from the presence of zebras in very coarse grassland types and the Masai have long recognized that the zebras' clipping away of the coarser growth, like fire, actually makes the foliage more accessible to cattle.

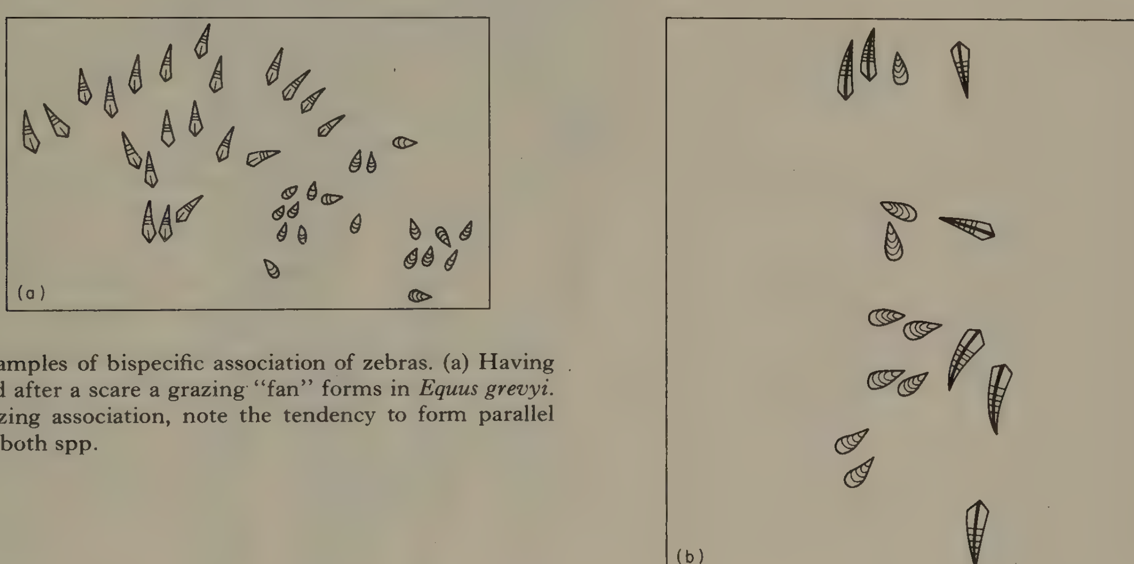
The zebras' relationship with the other major grazing species is therefore likely to combine complementary and competitive elements. Recognizing that the common zebra interacted in both ways with the other herbivores of the Serengeti, Bell (1969) examined the use of the environment, the movements and the spatial distribution of the Serengeti grazing community. In quantifying the degree to which common zebras associated with three of the commonest bovids, he found a close correlation between seasonal changes in the productivity of the vegetation and the frequency of associations. His coefficients (calculated by the method of Cole (1949) and derived from aerial counts) showed that degrees of association depend both on the structure of the vegetation and the tolerance of it by each species of grazer. The figures also showed that the zebra is the most social of the four animals.

Coefficients of association in Serengeti (1966—67) from Bell (1969)

		Wet	Dry
E. quagga	*Gazella thomsoni*	0·498	0·254
	Connochaetes taurinus	0·218	0·607
	Syncerus caffer	0·382	0·241
S. caffer	*Gazella thomsoni*	0·2	0·034
	Connochaetes taurinus	0·029	0·388
C. taurinus	*Gazella thomsoni*	0·369	0·137
	Syncerus caffer	0·029	0·388



Equus grevyi resting association with six giraffes.



Two examples of bispecific association of zebras. (a) Having clumped after a scare a grazing "fan" forms in *Equus grevyi*. (b) Grazing association, note the tendency to form parallel pairs in both spp.

Neither facilitation nor a common food supply can be invoked to explain the fact that both zebra species associate with browsers such as eland or giraffe, but they are, nonetheless, frequent companions. In the area of overlap between *E. grevyi* and *E. quagga* the two species commonly graze, walk and rest together, sometimes for successive days at a time, an easy association between the species that is all the more striking since their social organizations are very different.

No wild hybrids between *E. grevyi* and *E. quagga* are known and I am unaware of successful crossing having been achieved in captivity. It is interesting therefore to find that a wild Grevy's zebra can sometimes take an

intense and perhaps sexual interest in domestic horse mares even trying to circle and herd an animal with rider (Craig, pers. comm.). On Mt Kenya Hook (pers. comm.) bred numerous hydrids from a Grevy's zebra stallion and domestic mares. These "zebroids" have proved to be sturdy pack animals (see p. 138) and are usually larger than both parents but apparently always sterile.

There have been several reports of feral donkeys running with common zebra herds in East Africa but without breeding. Crosses have been frequent in zoos and Darwin (1868) described seeing a triple hybrid between a bay mare and the fertile offspring of a jackass and a female zebra. If female mules are fertile they reproduce the chromosomes of the father, whether jackass or stallion, effectively backbreeding to a pure parental stock or they have 63 chromosomes like their mother and remain a mule.

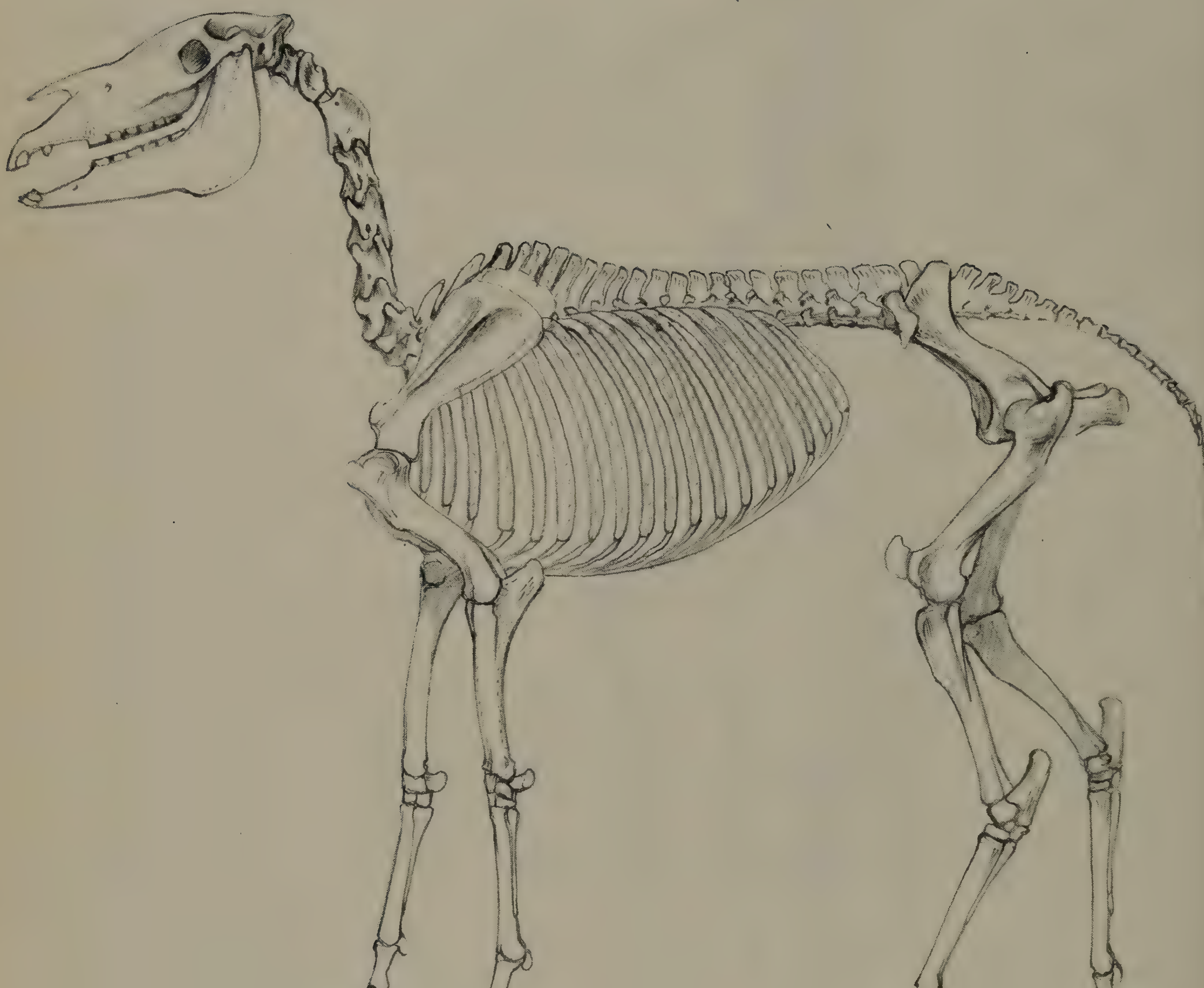
The breeding of horses, donkeys and mules was almost universal in the northern hemisphere and the horse has been intimately involved with man's development of civilization, so it is ironic that wild horses should have been exterminated wherever civilizations have flourished. Africa today is the last stronghold of wild horses, with four distinct species and numerous races. Outside Africa only one wild horse and one species of ass exist, and they hover on the brink of extinction. It should be remembered, however, that before the Neolithic period horses were dominant animals over most of Eurasia. For Palaeolithic hunters horses were a major source of food but, with the Neolithic and settled cultivation, horses must have become a major pest and eventually a competitor for the land, simply because they were numerous and difficult to deal with. In a vastly condensed manner the history of their extermination as wild animals is being followed in Africa today.

Pastoralists are generally tolerant of zebras (indeed, they are the epitome of beauty for the Karamojong) but this is not true for the farmer or settled rancher.

As settlement takes over more and more land, the mobile and persistent zebras still find their way back through all manner of obstacles to eat crops and consume grazing and water. The conflict becomes progressively intensified because pioneer settlement and ranching schemes start with a water supply and water is essential to the common zebra and as the distribution maps suggest (pp. 148) the last decade has probably seen a greater reduction in zebras than throughout the century. Sadly it is a decline that can only continue.

Equus grevyi, Equus quagga, Equus asinus, Equus caballus.

Overleaf: *Equus grevyi*



Grevy's zebra, Somali zebra (Equus grevyi)

Family Equidae
Order Perissodactyla
Local names
Damer feru (Somali), Haree (Kilianguli), Loiborokurum (Samburu).

Measurements
head and body
250—300 cm
height
145 (140—160) cm
tail
38—60 cm
weight
430 (380—450) kg males
386 (352—450) kg females
Average biomass weight
360 kg

Grevy's zebra, Somali zebra (Equus grevyi)

This species is the "Hippotigris" of the Roman circuses and was pictured in mediaeval works long before being named by Oustalet in 1882 after the President of France, who had been presented with a living one by Menelik, Emperor of Ethiopia. In 211—217 A.D. these zebras were paraded in Rome pulling ceremonial carts.

This long-legged zebra is very much more uniform in pattern than the common zebra but, notwithstanding this, some individual variation in the width of the stripes is perceptible at close quarters. There are occasionally traces of "shadow stripes" and Percival (1928) shot a white morph with barely perceptible stripes.

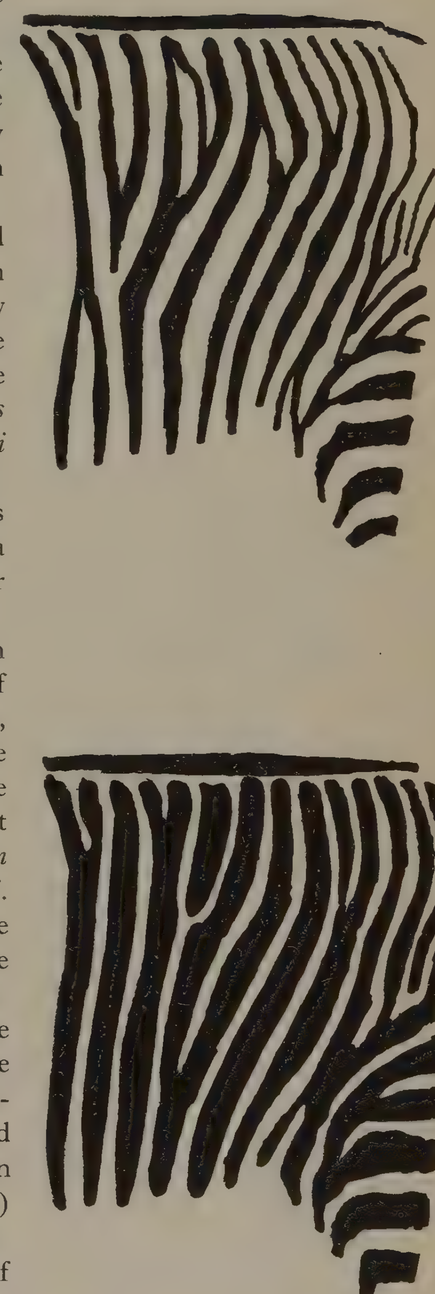
The broad rather circular ears, white stripeless belly and white-margined rump stripe are prominent specific characteristics. The head is larger in proportion to the body than in other equines and the skull is long and narrow with an elongated narial opening. These and other characteristics link the skull very closely with the Pliocene, *E. plicatus* in South Africa (which is the earliest member of the genus yet recorded in Africa), with *E. sanmeniensis* from the Early Pleistocene in China and with the more recent *E. valeriani* in Uzbekistan.

However *E. grevyi* is not entirely conservative because the braincase is somewhat enlarged. There can be little doubt however that this zebra represents the relic of a very ancient type of equine that once ranged over more than one continent.

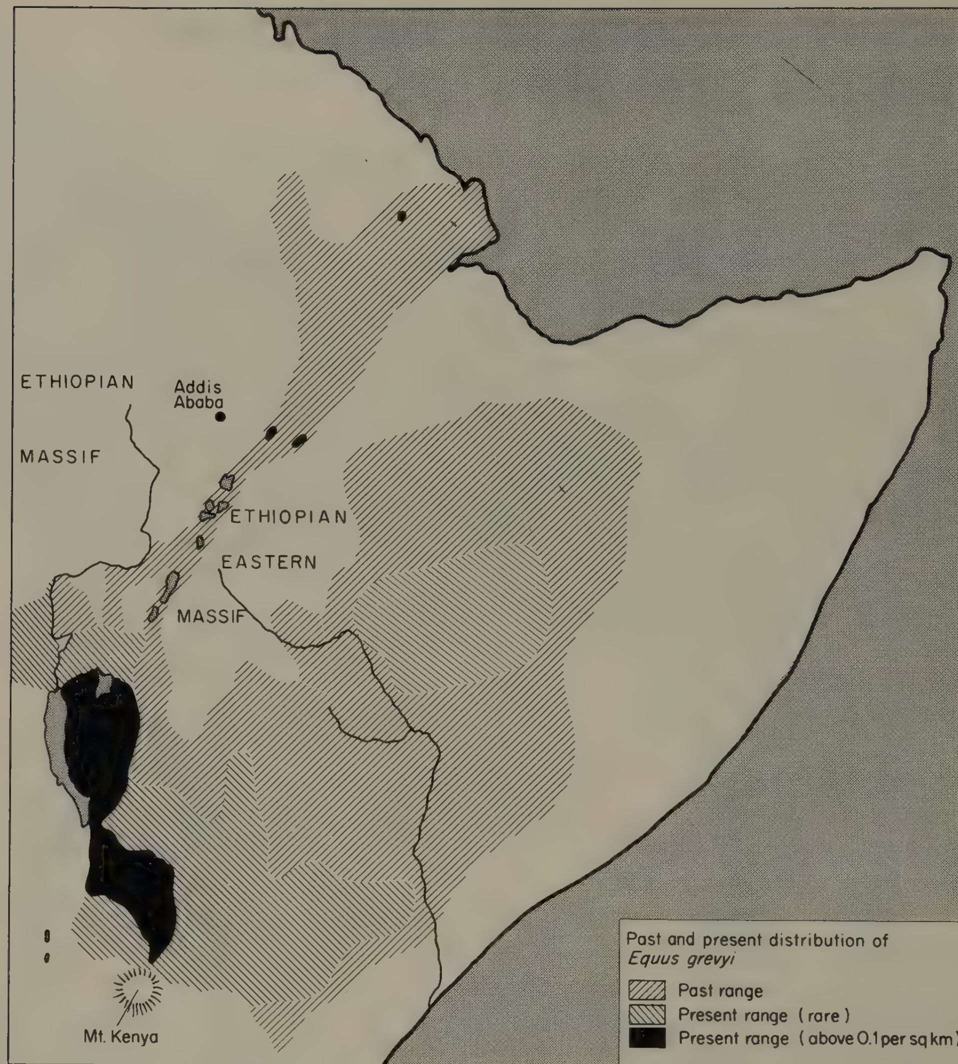
The main population of this species is now restricted to parts of northern Kenya with outliers in Ethiopia and, possibly, in Somalia. In the context of competition from other equines, the distribution of *E. grevyi* is significant, for it is wedged between the ranges of the arid-adapted wild ass and the water-loving *E. quagga*. Between the two extremes there exists an interzone where this small population of zebras has been able to hold its own against competition from both directions. The South African *E. quagga antiquorum* lives on the edge of the Kalahari in a somewhat similar habitat to *E. grevyi*. It is also puzzling that within historical times no zebras have occupied the long belts of what appears to be suitable country lying to the south of the Sahara, although asses once flourished in parts of the desert.

Equus grevyi is less dependent on water than *E. quagga*. Nonetheless, large numbers died during the 1950 drought in the Lorian swamp area and the seasons are sufficiently extreme within their habitat for most of the population to be forced to make local migrations in search of better grazing and water. During especially dry seasons large congregations used to gather in well favoured localities within daily reach of water, and Jackson (1894) described seeing them in thousands at Laisamis.

This zebra has seen a drastic decline in recent years, partly because of competition from local domestic livestock for water. Grazing is less problematic because the zebras can eat parts and species of grass that are inedible to cattle. In at least one locality in the south these zebras have expanded into the foothills of Mt Kenya in recent years and this has coincided with a succession

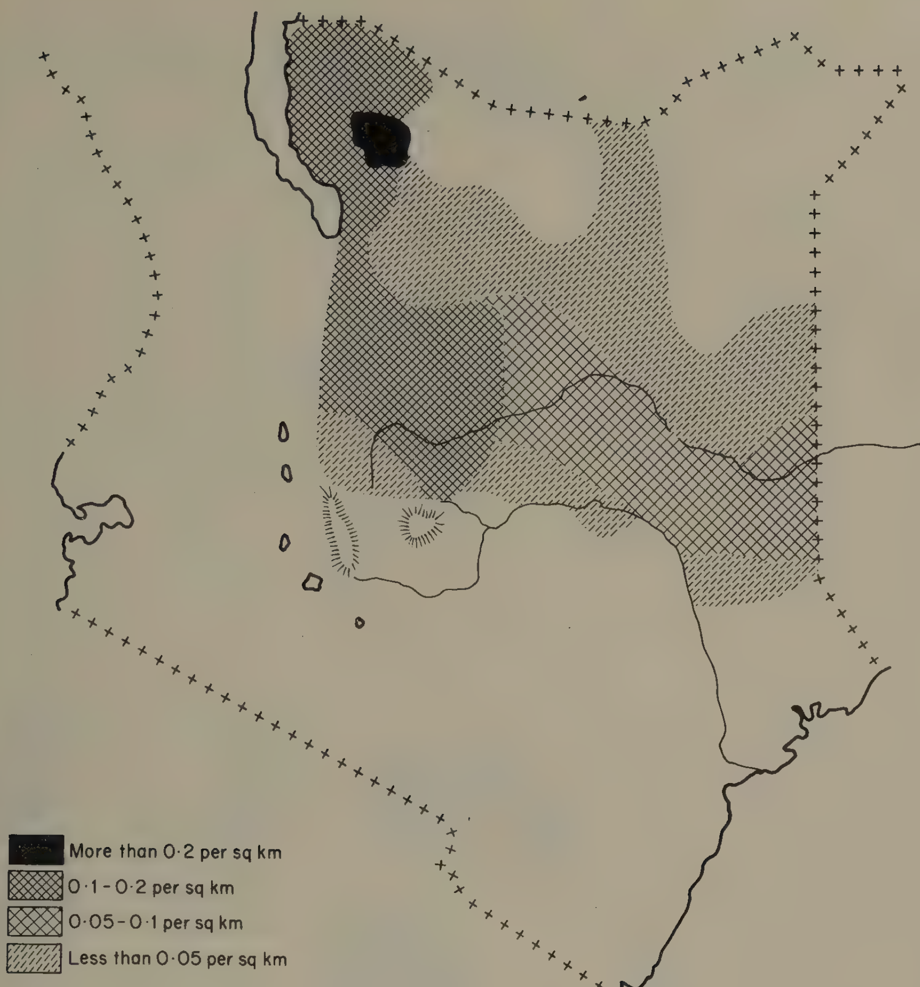


Variations in the width of stripes in *Equus grevyi*.



of drier years and the southward spread of a grassland type that is dominated by *Pennisetum schimperi* and *Eleusine jaegeri*; the former is a nutritious grass but is very tough and so is incompletely exploited by grazing ungulates. In the Lema Downs area the zebras are tolerated by the landowners and I found that the zebras were subsisting almost entirely on *P. schimperi*. There was a striking difference in the composition of plant fragments in the dung of cattle and zebras grazing on identical pastures, the latter containing much more of the hard fibrous stems. Other important grasses in their diet are *Chrysopogon ancheri*, *Cenchrus ciliaris* and *Enteropogon macrostachys*. This zebra has exceptionally abundant and long vibrissae round the mouth; plants, dung, urine and other substances are sometimes smelled very thoroughly with these hairs in contact with the object of interest. They are also probably stimulated by the activity of grooming.

This zebra's peculiarly open society was mentioned earlier (p. 131). The stallions on their territories and the mares with their foals are the most stable



Distribution of *Equus grevyi* in East Africa in 1977 (after Dirschl and Wetmore, 1978).

foci in the social life of Grevy's zebra. Males gather into bachelor groups; females also associate in nursing groups, and all classes of zebra may join up in large mixed herds. Klingel (1972) found that groups of homogenous composition, all-male, all-female or all nursing mothers sometimes maintained their identity, even when amalgamated with herds of up to 200 animals and he noted that nursery groups were common but unstable. However all these associations are unstable and animals move freely from one type of grouping to another. Dominance is inconspicuous or absent, except that a territorial male is very assertive of his mating prerogatives. Mares and the younger males move very much more freely than mature males, which become spaced out over vast areas as they become attached to particular territories. These are sometimes in regions that become uninhabitable during periods of severe drought and the males are eventually forced to leave. Depending on whether the entire population is nomadic or wholly resident or the males resident and the rest not, there are likely to be significant differences in the pattern of

social relationships and it would be interesting to learn more about the influence of local ecological conditions on the society, reproductive cycles and dispersal of these animals.

Where the stallions are forced to leave their territories, there is evidence of a seasonal peak in sexual activity beginning with the return of the males to their wet season range and a spate of fighting that may occur before or at the same time as the arrival of the mares. Depending on the local pattern of rainfall, this peak of territorial and mating behaviour seems to take place during the short but reliable rains of July and August or later during October and November, which also tend to be wet months. The worst time of the year is generally February, and if the April rains fail, as they sometimes do, the general condition of the animals and their habitat is unlikely to improve

for some months, which probably impairs their reproductive rate and encourages seasonal breeding. Klingel (1972) thought that irregular rainfall from year to year reduced the reproductive potential of zebras in his study area near Wamba because territories were apparently only established on the rainy season grazing range where the territorial males remained while females and non-territorial stallions emigrated. Klingel thought there would be few conceptions because there were no territories in the dry season areas to allow undisturbed mating. This meant that territorial males and females were segregated for part of the year limiting reproduction to the rainy season.

In fact an oestrous mare provides a powerful stimulus to any stallion and a female is unlikely to lack suitors. A scatter of foal sizes suggests that there is in fact some breeding going on throughout the year in many parts of northern Kenya and the dominant status of the stallions and reproductive success might not be tied to land tenure quite as strictly as was suggested by Klingel's observations at Wamba. Nevertheless, males generally space themselves out into two classes, territorial males and free-ranging subdominants that avoid confrontations with dominant males through submissive behaviour. Once established, this order seems to be maintained until the onset of the next major season of drought.

A resident stallion actively seeks the company of other males grazing in his area. Dominance is asserted by a proud posture with arched neck and a high-stepping gait (see margin). Submissive males extend their tails and lower their heads, then very briefly muzzle the superior animal in the chest or groin, a gesture that might derive from grooming or sucking behaviour but might also be an olfactory confirmation of status. The large dung piles made by Grevy's zebra might have both territorial and hierarchical functions.

Only the males drop their dung in one spot but the huge dung piles found near paths, waterholes and river junctions are apparently the result of more than one animal's activity. Certainly a site continues to be used year after year and it seems likely that the dung pile is added to by many of the males passing by, and it is possibly a focus for male activity in the region. It could allow transient and subdominant males to become acquainted with the signature of the resident stallion. The making of dung piles may be influenced by the presence of other males. A captive stallion living in a paddock with a small herd of females has never shown any sign of depositing his dung in one place. Likewise horses and other zebra species appear to make dung piles in the course of inter-stallion displays. Joubert (1972c) has suggested that defaecation by challenging *Equus zebra* stallions might have evolved out of a territorial organization. In this species one challenger defaecates or urinates after which the other moves to the spot, sniffs and superimposes his own contribution. Bachelors also defaecate in sequence on the same spot and Joubert thinks the sniffing may be a checking of androgens. No *flehmen* was observed in these rituals.

The stallion is only intolerant of subordinate males if there is an oestrous female in the vicinity, in which case he drives all other males off at a run with a typically equine rolling of the lowered head. He then becomes preoccupied with copulation and attempting to restrict the female to his own area. Having recognized that oestrous mares were the source of fights, Klingel (1969c) used his vehicle to herd oestrous females and thus provoke a series of

clashes. In this way he was able to map territories and discover their exceptional size, ranging from 2·7 to 10·5 sq km (average 5·75). Klingel recognized that an area of dominance functions as a mating territory in which the owner has exclusive rights and the value of the territorial system was revealed to him when observing an oestrous mare in a non-territorial area. "For hours she was courted by up to nine stallions at a time. These stallions were fighting each other almost continuously and therefore none of them succeeded in copulating with the mare. The group eventually moved into a territory where the territorial stallion took over. The other stallions moved away while he copulated with that mare undisturbed." When a stallion's interest in a mare is aroused (often by the sight of her urinating) he approaches with slow measured steps with his neck arched, chin down and ears pricked forward until they are horizontal. While the male investigates her, a mare sometimes sniffs or makes a short butt into his groin before turning away sharply. This sequence has some resemblance to the dominance rituals between males, and the first stages of courtship also seem to consist of a simple assertion of dominance. During the peak of mating activity the resident stallion takes an intense interest in the approaches of any other zebra, particularly small groups or scattered individuals. Horses also attract attention, and mounted riders have described being investigated by a hackney-trotting stallion circling them with arched neck and proud stance.

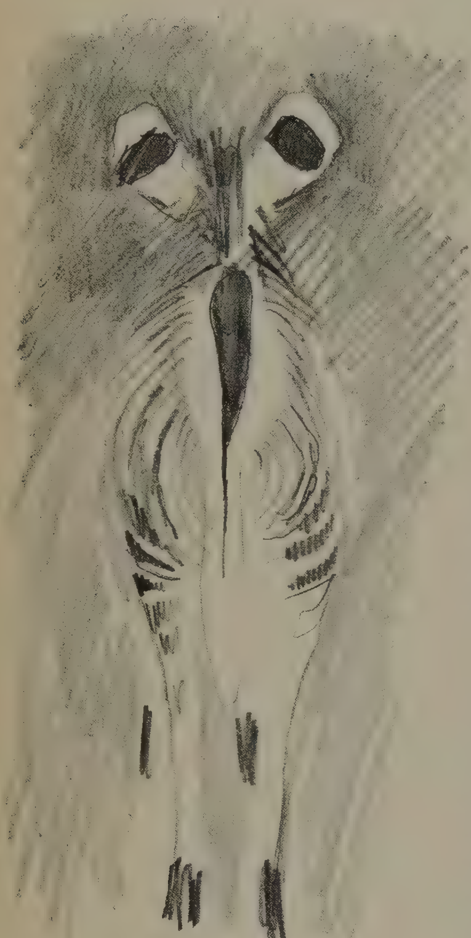
While courting and copulating, the male utters a very loud bray followed by a long strangled squeak. The same call is directed at other males and it has a visibly intimidating effect on the oestrous mare as well as other males. Both tend to avoid or appease the caller.

One manifestation of the stallion's attachment to his own area and of his intrinsic dominance is the fact that he stands his ground when there is an intrusion by other animals, humans or vehicles. Chronicles by hunters frequently describe Grevy's stallions as stupid because they seldom run far, then turn to face the disturbance and, therefore, get shot. Reluctance to flee

probably render them more vulnerable to carnivores but the killing of lions by stallions is not unknown and captive stallions are well known for their confident but normally unaggressive behaviour.

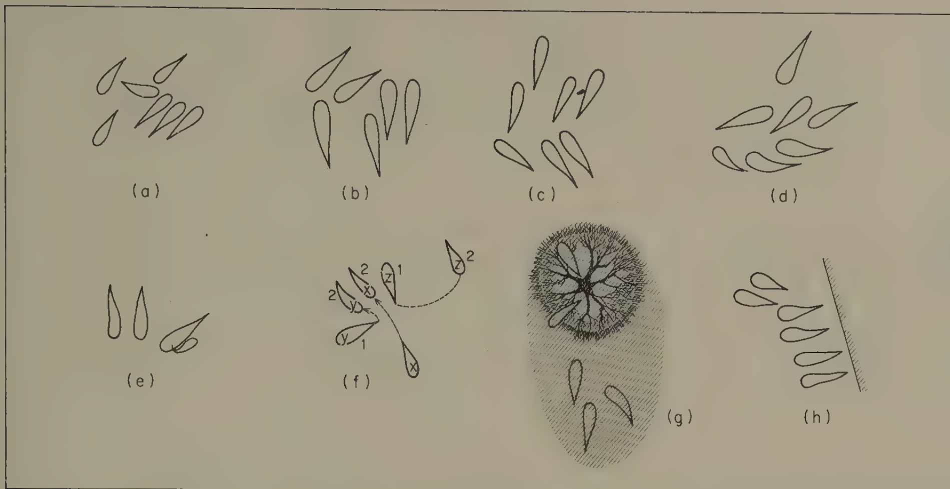
One informant described to me how he had been led by vultures to the carcass of a Grevy's stallion and an adult male lion. The latter had been bitten in the small of its back which had apparently severed the spinal chord; both animals had died of their wounds.

According to Klingel (1969d), gestation is about one year but Riley (in Groves, 1974) estimated 390 days.

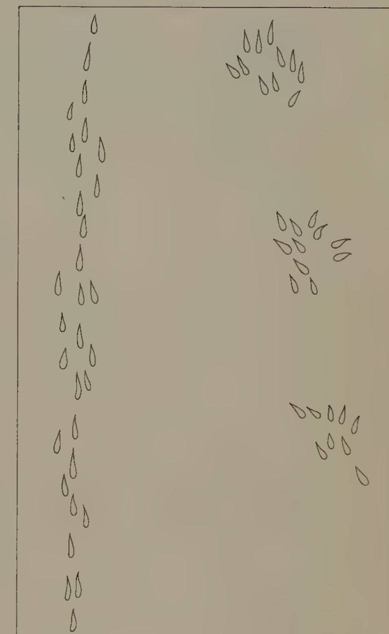


During the first few days after giving birth, the mare drives off any other zebra approaching her young. An extraordinary continuation of the mane down to the root of the tail is one of the most striking characteristics of the foal and there is another crest of hair down the midline of the belly. As it grows older, the dorsal mane gets thinner, shorter and darker but during the first months of life it is slightly erectile, standing up when the animal is excited and lying smooth when relaxed. The mother often rubs her chin and neck over the foal's back and sometimes nibbles at the mane, so its main significance might be to stimulate direct contact. The newborn foal is russet brown and white but the white tips of the ears have a strongly contrasting black margin which gives great emphasis to ear movements. The neck stripes are the first to alter from their baby russet to black at about four months; thereafter the change from long fur to short hair and adult colouring is relatively rapid. The posterior section of the dorsal mane, where the black stripe stands out against a pure white rump, eventually becomes the most conspicuous and distinctive signal pattern of an adult Grevy's zebra. This long range signal might mimic the mare's crotch, for the latter is a most compelling focus in the foal's life and social cohesion could be well served by the evolution of an adult equivalent and mock continuation of this infantile attraction. When walking in line foals follow every detail of their mother's course and in spite of her concealing tail the line of the black genital skin stands out very well from the pure white thighs on either side. Also, the young often sucks from behind.

The development of social patterns around parent–young, sibling or male–female relationship is often reflected in the spatial dispersal of animals. For social herbivores the thoroughness with which they graze an area may be influenced by their dispersal patterns and Grevy's zebra is specially interesting in this respect.



Four examples of zebras resting in the heat of the day (in light scrub) (a—d). (e) Three females resting one with nursing foal. (f) Displacement of one female (z) by another (x). (g) Resting group standing in tree shade. (h) Grazing group stopped by steep bank.



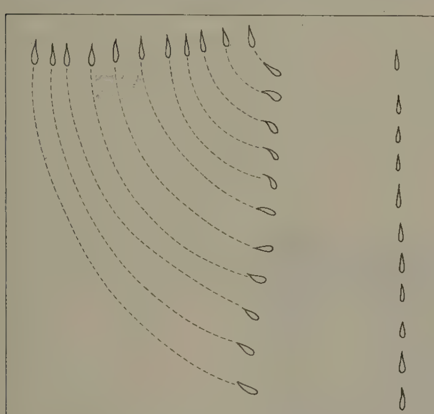
(b)

(a)

Above: On being disturbed a group canters off in linear formation, they slow to a walk and as individuals stop, distinct clusters (b) form as animals behind come to a halt beside those ahead of them.

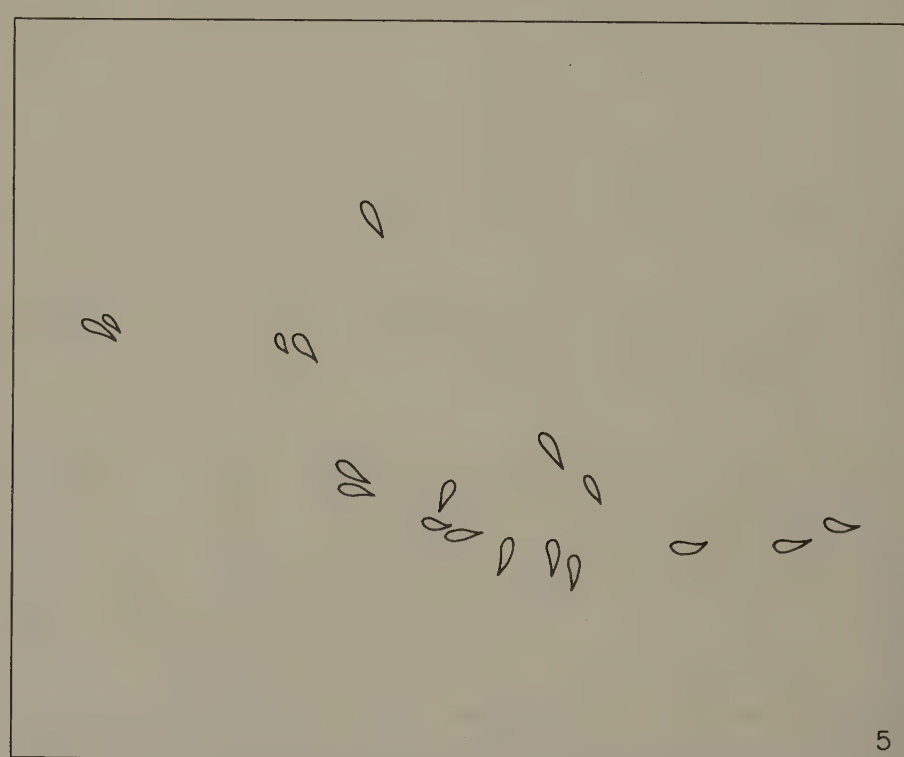
(a)

(b)



Right above:
(a) Grazing along a broad front the zebras reach the crest of a ridge, sight a distant herd of cattle and (b) all turning right, move off in line.
Left above:
(a) A long line of female zebras walks and trots through bushy country.
(b) On emerging into open grassland all the animals stop, turn 90°, start to graze. As each animal tries to move up beside its nearest neighbour the effect is for the grazing front to swing forward like a spoke on the vortex of the leading animal.

The linear walking pattern possibly derives from the mother–young relationship. This can readily change to a skirmishing line either by a synchronized right-angled turn or by the front animal's stopping and the others coming up and ranging out side by side. This is commonly seen on cresting a rise or on arrival at a new pasture. As the herd grazes, a wedge may form, but this soon dissolves as the grazers wander at large. When a grazing animal begins to get isolated from other zebras it generally casts its head around until it has seen another animal and then alters its line of graze to bring it back towards its fellows. There is normally no competition for grazing but captives, attracted to a single source, such as a handful of grain, may fight over it. When an alarm alerts a line of zebras, they all face it side by



1 Line of walking zebras breaking up as they begin to graze

2 Zebra grazing in a dry watercourse

3 Galloping in a clump on being buzzed by an airplane

4 After clumping and then stopping, a return to grazing

5 Temporary clump begining to disperse

Grevy's zebra photographed from the air September 1975.

side snorting; and at a sound or movement from the enemy they may turn about and gallop off quickly, bunching as they go; but this soon changes and a return to single file indicates that the alarm is over.

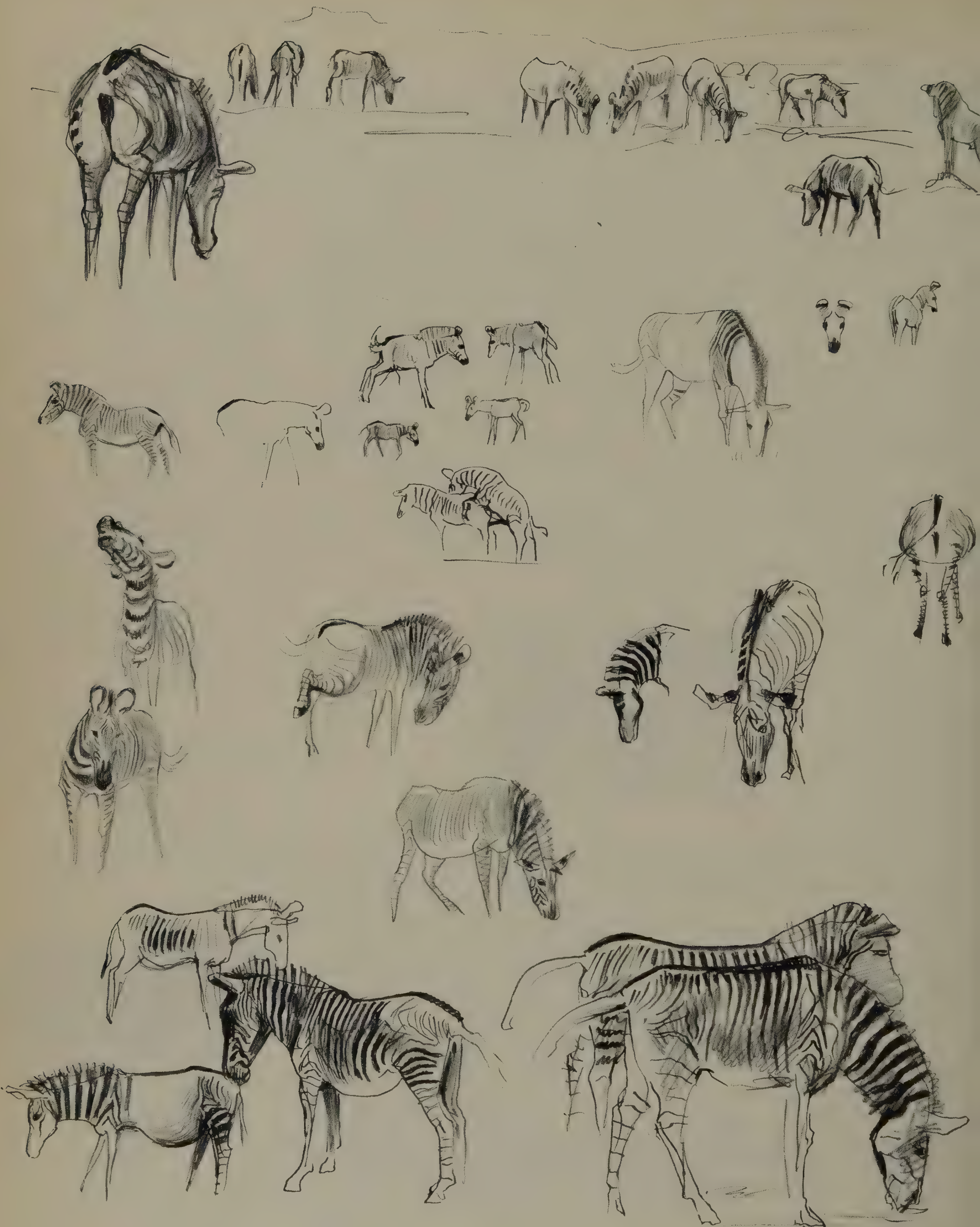
The tendency to bunch in response to disturbances is common to all equines and the more intense the alarm the tighter the formation. In Grevy's zebra there are also situations where scattered animals can be seen to draw together into a recognizable unit. This is noticeable as they approach water-holes or form mixed associations with other animals.

The readiness of a zebra to take flight depends on many factors, including the obvious influence of shooting or other predation. Fleeing distances diminish the longer the animals go without grazing, and the proximity of other species, such as giraffes, also makes them less wary so long as their companions do not become alarmed.

If a zebra is slightly disturbed during grazing it raises its head repeatedly with a backward flip and flashes its ears. Other ear signals are apparent in the round discs of an alert facing animal and a horizontal "rowing" action from a more relaxed animal about to make a move.

The ears are pulled back and the teeth bared in threat, while the tail is arched in the air. A very rapid swishing of the tail often precedes threats and this visual and acoustic signal causes foals to draw in close to the mother's side. An animal on the defensive may simply turn its back and raise a hindleg in preparation for a kick; at higher intensities it lashes out with both hindlegs. Rearing up and flailing with the forehooves is generally restricted to males. Fighting zebras are often forced on to their knees or haunches by the antagonist going for the legs; when trying to bite each other's necks the heavy heads and muscular necks are wrestled, in the course of which an opponent's head may be pinned down to the ground. Necks, withers, and croup are commonly scarred from bites.

Resting heads on shoulders and rumps is much rarer than in *E. quagga* but it may be adopted when groups gather together in thorn scrub to rest during the heat of the day. At this time there is a tendency to adopt a star formation but there is also a distinct trend towards pairing within the group.



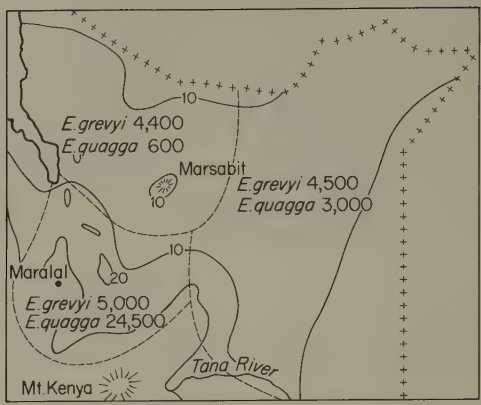
The equine habit of forming partnerships is manifested in a temporary form whenever groups become small and scattered and the males that get left behind by the main herds during the dry season often pair up and have even been seen to groom one another (Rainey, pers. comm.). Grevy's zebra are also unusual in that a female with a newborn foal seems to prefer the company of another new mother and the two adults may remain close in spite of being intolerant of one another's offspring.

When following the mother, the foal's principal cue seems to be the sight of her tail. At rest the mother is a focus of continuous interest, heads are frequently rubbed together and in the course of mouth-to-mouth nuzzling very young foals may tug at the mother's long oral vibrissae. In the absence of another colt to play with, older colts tend to bully their mothers, with ears back in pseudo aggression the youngster will rub, nibble, tug and bite at its grazing mother's legs, neck, shoulder or flanks. The penis of a young colt is already conspicuous and mobile at the age of a few months. The short neck and long legs of foals require them to splay their forelegs widely to reach the ground and the younger ones display little interest in grazing.

In spite of remaining with their mothers for up to three years, colts tend to become relatively independent at about seven months. Even at one month or so foals will remain alone while mothers graze some hundreds of metres away and Klingel found foals on their own while their mothers walked many kilometres to water. Mothers with new foals tend to avoid large mixed groups and temporarily join other mares with very young offspring. I found some of these new mothers in small groups particularly reluctant to part from one another or, in one case with the herd of giraffes they were accompanying.

In spite of the isolation and part independence of foals, it is possible that the former offspring readily rejoin their mothers, for I saw one heavily pregnant female that was consistently followed for two days by a large juvenile as well as a subadult.

Although both sexes are capable of breeding and three-year-olds have done so in zoos, both Klingel (1974a) and King (1965) agree that wild Grevy's stallions do not mature until they are about six years old.



Relative numbers of *Equus grevyi* and *Equus quagga* in north-eastern Kenya in relation to 10 m (250 mm) isohyets. Broken lines delineate census areas. (After K.R.E.M.O. Aerial Survey)

Once common in southern Ethiopia (where Galla horsemen used to kill them in order to decorate their horses' necks with the striped mane), they now occupy mere fragments of their former range. Kenya is the last stronghold of this species.

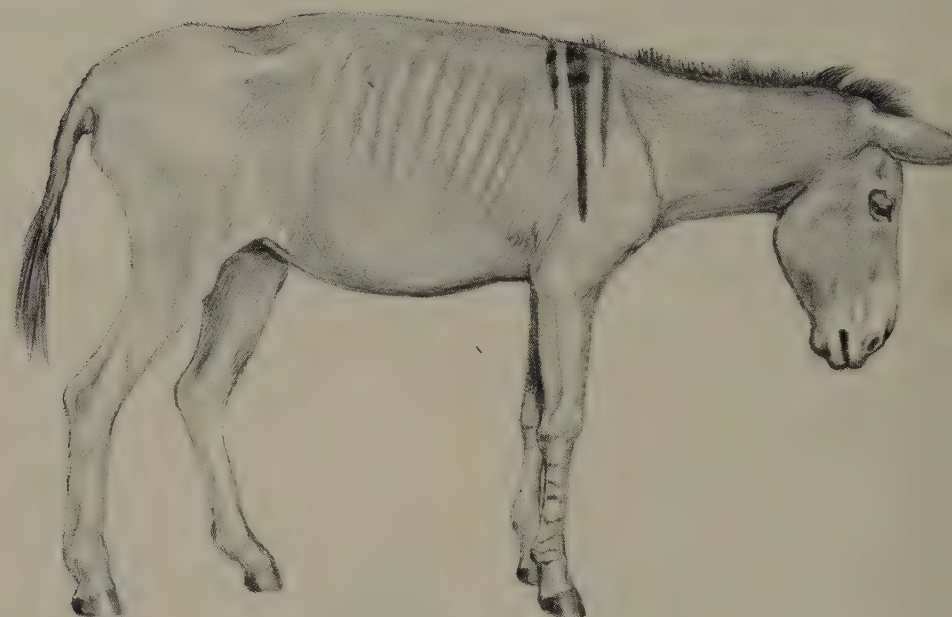
An interesting light is thrown upon the status of this declining species when it is remembered that less than a hundred years have passed since its first scientific description, which is rather few zebra generations—one in the London zoo lived 22 years. Their decline will undoubtedly be hastened now that major ranching schemes are being developed in the choicest areas of their range.

Detailed comparisons of their ecology and behaviour in the moister and drier extremes of their habitat would be especially valuable, but Klingel's work has shown that wide-ranging, long-term studies are likely to be beset by numerous problems. The animals have large ranges and seldom restrict their movements to protected areas and the recognition of a large number of individuals is essential. Some of the branded animals from Klingel's study are known to have ended up as trophies partly because they had become used to a vehicle. Such hunting clearly defeats the purpose of Klingel's important and continuing pioneer study. More recently a cowboy-style game-catching unit moved into Rainey's study area south of Maralal and was actually televised capturing animals, some of which had been habituated in the course of Rainey's long-term studies while others were dispersed or seriously disturbed. Norris (1976) has drawn attention to a report that licences have been issued to individual dealers for as many as 200 Grevy's zebra skins at a time. At current prices the beneficiaries of such largesse stand to earn profits of over one million shillings. It will be a sad and condemning reflexion on the values of our civilization if one of the most beautiful and interesting of all mammals becomes another victim of the current indiscriminate rush to exploit East Africa's natural resources.

In March 1978 the Ministry of Tourism and Wildlife proposed to set aside a former cattle holding ground between Maralal and Rumuruti as a permanent Grevy's zebra reserve and this may help to halt the current decline of this species. The Lake Turkana National Park also embraces an important Grevy's zebra habitat. In March 1978, the Ministry published the results of an aerial survey (see map) and pointed out in a press release that there had been a 65% decline in numbers in the Samburu–Loroghi plateau area in the last seven years. A projection of this rate of decline would culminate in extinction by 1985.

In 1977 the Ministry's Rangeland Ecological Monitoring Unit counted 287 animals in a 2% sample of potential habitat and the total numbers in Kenya rangelands have been estimated at 13,718. Regular counts are planned in the future.

Domestic Equines
(Equus asinus, Equus caballus)



Ass, Donkey
(Equus asinus) (domestic and feral)

Horse, Pony
(Equus caballus) (domestic only)

Common zebra, Painted quagga (Equus quagga)

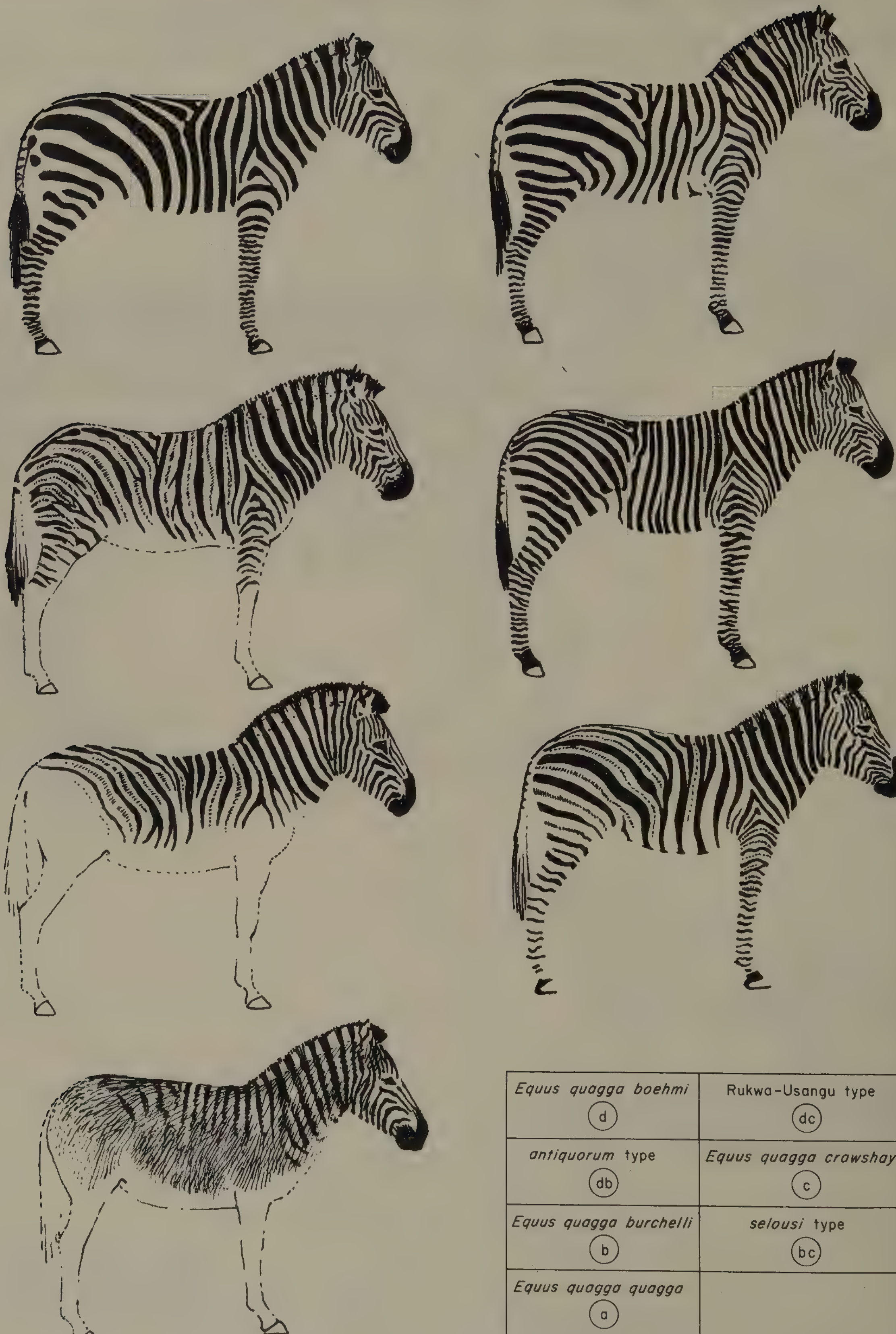
Races

Equus quagga boehmi
Equus quagga crawshayi

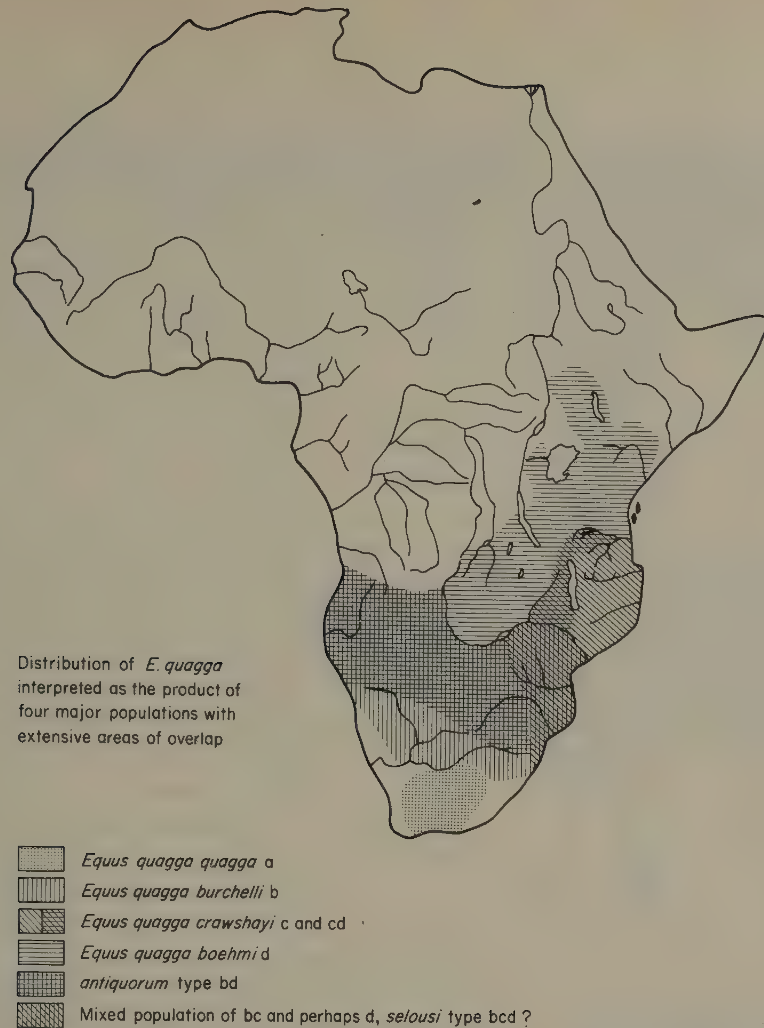
Common zebra, Painted quagga (Equus quagga)

Family Equidae
Order Perissodactyla
Local names
Punda milia (Kiswahili), Itiko (Kichagga), Eutulege (Luganda, Runyoro), Etuko (Karamojong), Lagwar (Lwo), Entorege (Runyankore), Injiga (Ishinyika), Hares (Kiliangulu), Eloidigo (Masai).

Measurements
head and body
217—246 cm
height
127—140 cm
tail
47—56·5 cm
weight
250 (220—322) kg males
220 (175—250) kg females
Average biomass weight 200 kg



Equus quagga boehmi (d)	Rukwa–Usangu type (dc)
antiquorum type (db)	*Equus quagga crawshayi* (c)
Equus quagga burchelli (b)	*selousi* type (bc)
Equus quagga quagga (a)	

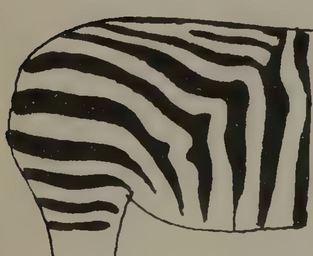


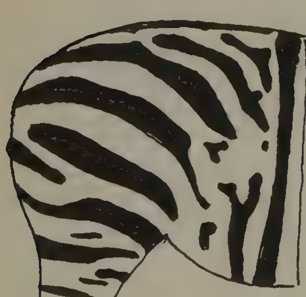
Distribution of *E. quagga* interpreted as the product of four major populations with extensive areas of overlap

Common zebras once ranged throughout eastern and southern Africa except in areas that lay within former forest belts, as in western and central Uganda. Within this vast range several populations can be identified as well as a latitudinal gradient in which striping diminishes in extent towards the south.

The most abundantly striped race *E. q. crawshayi* occupies the Mozambique zone, an area with a slightly impoverished fauna that may have suffered some isolation in the past (see Volume II, pp. 3, 42, 382, 400). The lack of an infundibulum in the lower incisors of zebras from this area tends to confirm the likelihood of a past isolation. These zebras inhabit miombo woodlands between the Rufigi and Zambesi rivers and their western boundary follows the Muchinga escarpment. Throughout the rest of eastern and central Africa the zebras have equally complete striping of the body head and legs but the bands are fewer in number, sometimes almost half as many, and therefore bolder in effect. This race, *E. q. boehmi*, inhabits various wooded grasslands but generally lives in more open country than *E. q. crawshayi*. Along the margins of the Mozambique zone and across a broad belt of south-central Africa, zebra herds often exhibit a mixture of morphs and individuals and commonly have bold, widely spaced black stripes with fainter brown lines or "shadow stripes" in between, almost as though bold stripes had been superimposed on a fainter many-striped format. This trait is rarer in equatorial zebras.

Distribution of *E. quagga* interpreted as the product of four major populations isolated during a moist period





In the temperate grasslands of the high veldt in South Africa there used to be a distinctive population of zebras, *E. q. burchelli*, in which the stripes on the rump were attenuated and the legs were white and normally without any stripes. Animals approaching this condition still exist in the western Kalahari and in Zululand but they represent one extreme in a large and variable population that ranges from the eastern low veldt across the Kalahari to Angola. Commonly identified as *E. q. antiquorum*, *E. q. chapmani* or *E. q. wahlbergi*, this is essentially a mixed population, very frequently "shadow-striped" and with a degree of striping on the legs that tends to increase with proximity to *crawshayi* and *boehmi* in the north and decrease towards the south, a variation that is sometimes held to illustrate a cline.

In the southern tip of Africa the extinct Cape quagga's range used to correspond very closely with that extraordinary island of desertic vegetation, the Karoo. There can be few sharper contrasts in environment than that presented by the moister, sometimes subtropical areas of the eastern Cape and the arid Karoo, so it is not surprising to find there an endemic flora and fauna that has become specially adapted to low rainfall and severe winter frosts. The quagga was a clearly differentiated population and remained restricted to the immediate vicinity of the Karoo, no physical barriers separated it from the neighbouring Burchell's zebra and Barrow (1801) reported seeing herds of quagga and zebra together. As regional populations of *E. q. boehmi* are known to maintain a high level of distinctness in spite of overlapping ranges, this cannot be taken as proof of specific difference. Nevertheless, the quagga represented a peculiar ecological isolate of the common zebra although it might be regarded as having been an incipient species (see p. 139).

In addition to regional or ecological differentiation in the common zebra, a description of the pattern must take account of individual variations in the relative width of black and white stripes. In most animals the proportions of black and white are even but in those individuals in which the stripes are wider or narrower the general impression is of a lighter or darker animal because all the stripes conform to the same trend. The illustrations show some extreme examples of this phenomenon in *E. q. boehmi* from East Africa but I have been unable to see examples of an all-white or even near-white zebra, although they have been reported in Tanzania by Teare (in Bourdelle, 1949). Variation in stripe width occurs in all zebra species and the striking variants of Cape quagga (see colour plate) were probably influenced by this phenomenon.

Aberrations of pattern (colour plate) in which there is spotting or marbling may have quite different genetic origins to these variations in stripe width, although there is a tendency for narrow black stripes to break down into spots. Since vertical trunk stripes and horizontal leg stripes are arranged differently in each species of zebra, it is interesting to observe considerable variation of pattern on the rumps and flanks of common zebra. Spotting or "dislocation" often occurs where the two stripe systems meet (see opposite).

The present range of common zebras stops short of the Sahara and no zebras are found west of the Nile. However, there is evidence of their occurrence in Algeria during the Neolithic (Groves, 1974) so that their extinction in

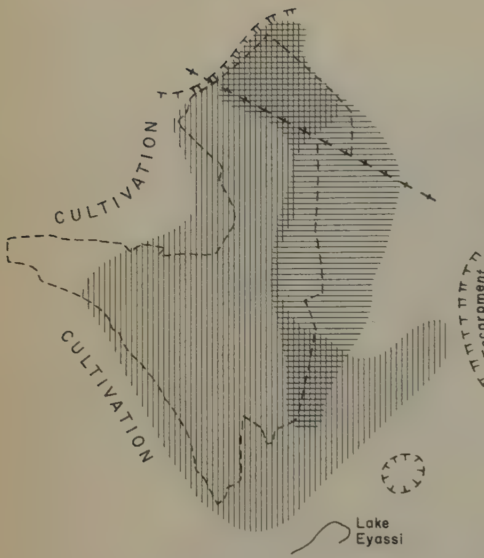
facing page: Variations in width of zebras' stripes

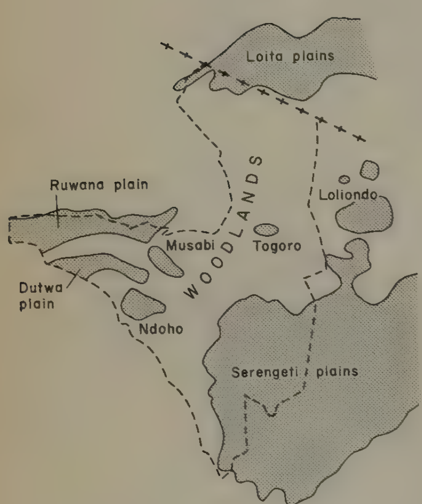
northern and perhaps western Africa may be relatively recent although they do not appear in the numerous rock arts of the Sahara.

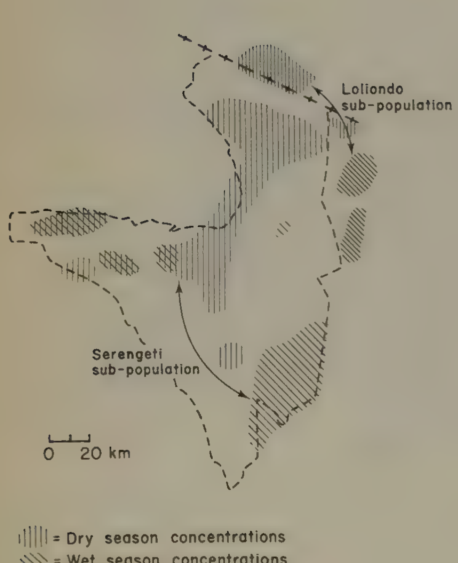
In East Africa, zebras are increasingly restricted to parks, sanctuaries and game reserves. The dependence of this species on water has already been mentioned and this certainly puts limits to its range. Another factor influencing the zebra's overall and seasonal distribution is the condition of the soil, for it requires reasonably firm ground underfoot.

As far as food is concerned the zebra's success is undoubtedly assisted by its lack of selectivity. Casebeer and Koss (1970) have found that the zebra's diet approximates to the actual grasses available, although the dominant fire-climax grass, *Themeda*, figures very highly in stomach samples. Vesey-FitzGerald (1965) noted them favouring *Sporobolus* and freshly growing *Vossia* in the Rukwa Valley. They are also adaptable grazers, mowing short lawns close to the roots but equally able to take taller flowering grasses at a higher level. Sometimes they will also use their hooves to loosen grass roots systems and rhyzomes. Gwynne and Bell (1968) found Serengeti zebras tending to graze on grass stems and sheaths, Lamprey (1963) estimated that 92·5% of their food was grass, about 5·4% herbs and 2% shrubs. When the first green flushes appear at the end of the dry season the zebra's movement on to new pastures becomes conspicuous when resources are on a large scale as on the Serengeti plains. Together with the gnus, zebras can be seen moving on to the well drained flats and, as the family units coalesce, tens of thousands may congregate there during the wet season. However, in many other areas it is primarily water shortage that causes zebra concentrations during the dry season, mainly along the lower lying drainage lines. Many of these areas become waterlogged when rain falls, whereupon the zebras immediately get on to higher ground and disperse over better drained pastures in the woodlands. This pattern of seasonal movement is most apparent throughout the miombo (*Brachystegia*) and *Acacia*, woodlands.

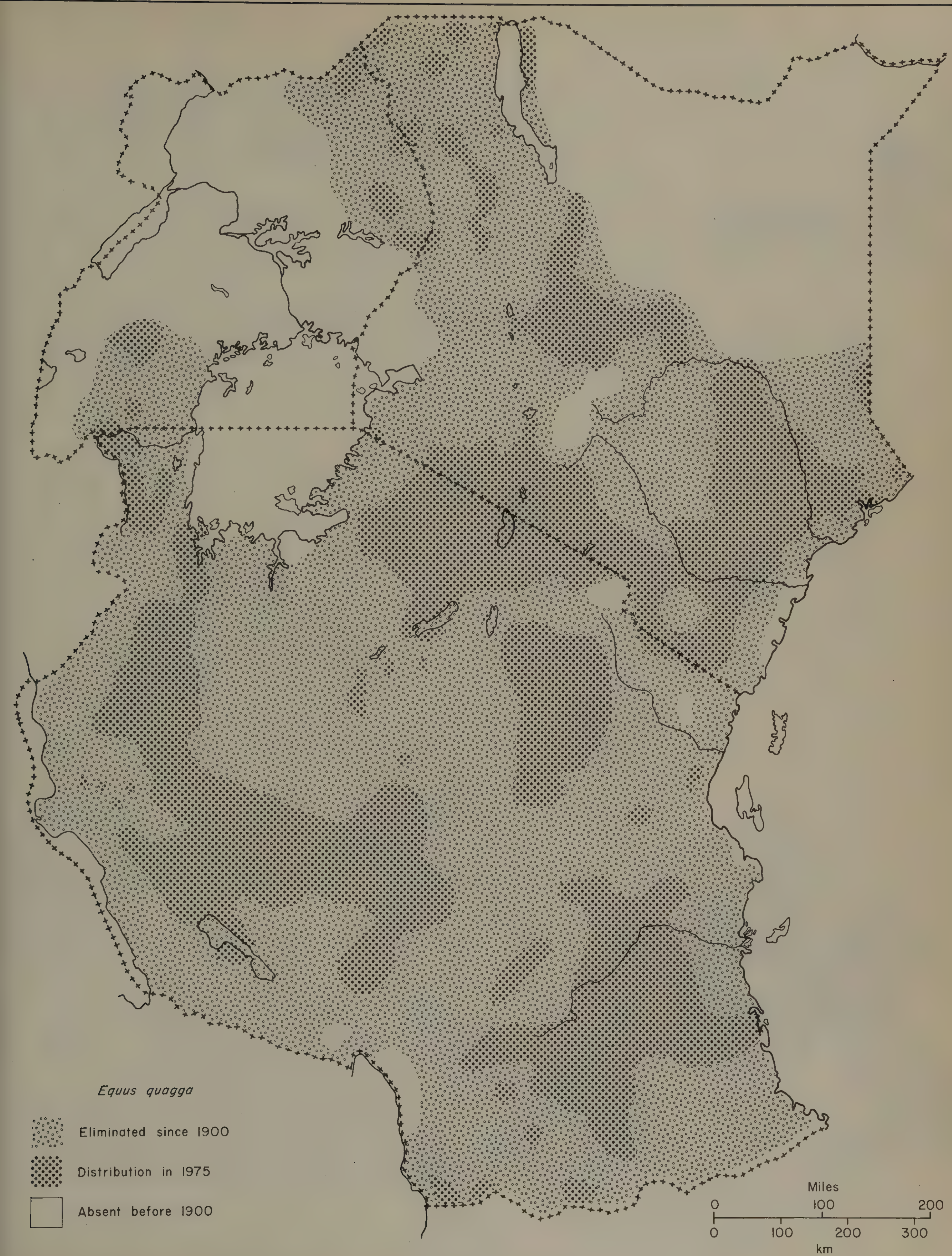
In Ngorongoro about 5,000 zebras are concentrated on the crater floor during the dry season but Klingel (1964a) found them dispersed over an area four times as large during the rains. Thus densities of zebra fluctuate seasonally and the total home range of a single family group is also subject to considerable variation according to the local ecological conditions. Klingel (1969c) has plotted and mapped the yearlong home ranges of several Ngorongoro families, but in places with less favourable conditions very much larger areas are used. In particularly favourable areas such as Serengeti, zebras may reach an overall density as high as 5·8 per sq km. In the Serengeti Park it is only during the rains that the zebras stop moving and this is because the plains are a homogenous habitat with water universally available in scattered pot holes.







Above: Distribution of the Serengeti and Loliondo sub-populations of zebras. (From Skoog and Gogan, 1975.) Loliondo was occupied by approximately 30,000 zebras (1968—71) in the wet season; these move north, in the dry season, as far as Loita plains. The Serengeti sub-populations (some 100,000 in 1968—71), leave the Serengeti plains in the dry season and according to Skoog, constitute a distinct but overlapping population.
Centre: Serengeti National Park showing grasslands.
Below:
Serengeti National Park—zebra concentrations. (After Kruuk, 1972).

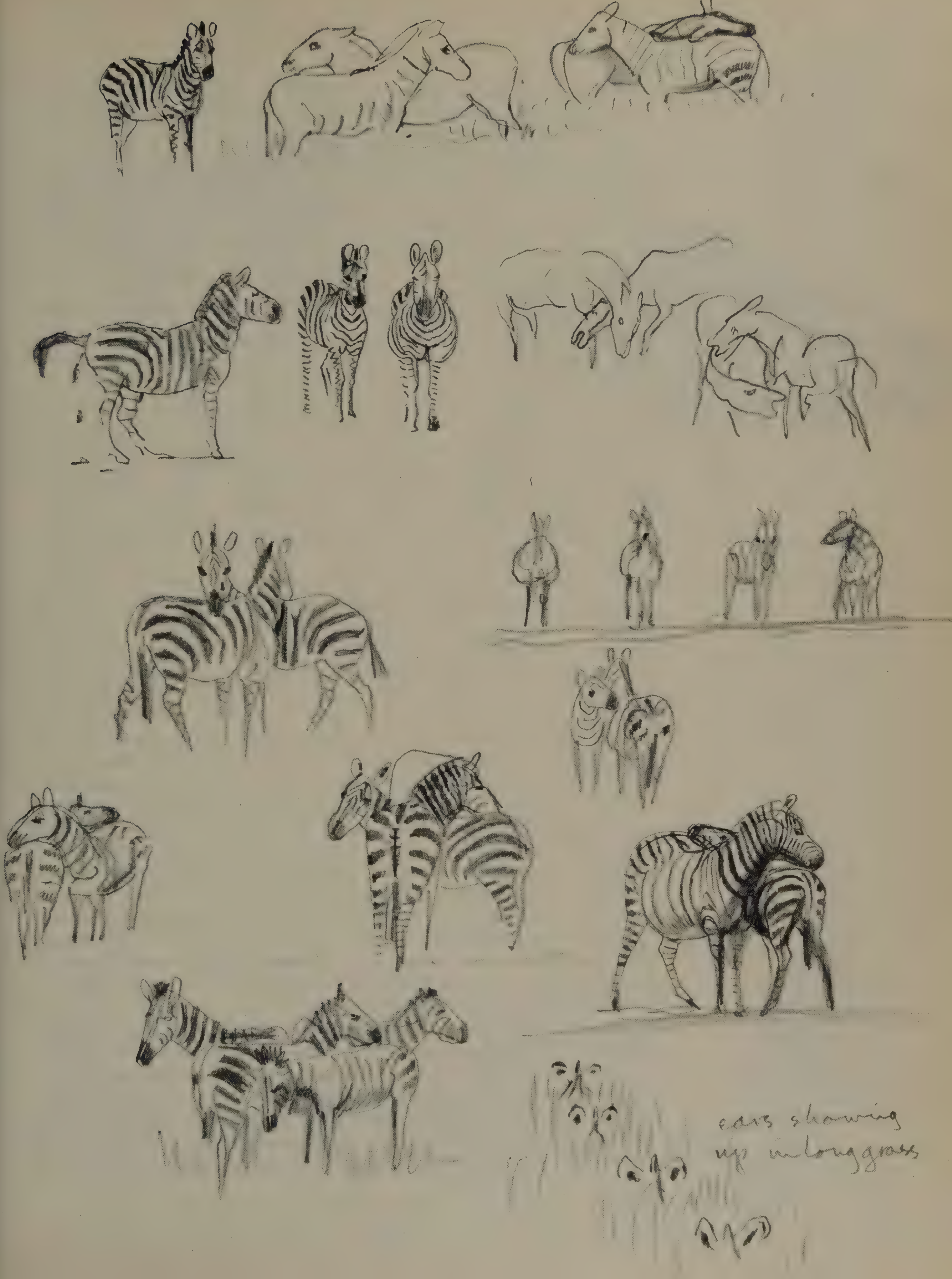

Equus quagga
Eliminated since 1900
Distribution in 1975
Absent before 1900
Miles
0
100
200
0
100
200
300
km

The zebras' daily activity is normally dominated by movements from open short-grass areas on higher ground that are used as sleeping or resting areas and pastures that are sometimes on lower ground and as much as 13 km away. Grazing is reached along well trodden paths without much dawdling on the way.

The choice of night resting spots may be influenced by a variety of factors and the type of terrain used may vary with the locality. For instance, on Mt Kenya I found a small zebra group habitually sheltering in the lee of a dense thicket which afforded them protection from the wind but also a clear view over the valley below. Verheyen (1951) noted them withdrawing into wooded valleys in Upemba and attributed this to avoidance of lions and shelter from the cold. On moonlit dry nights zebras can be quite active. Klingel (1967) noted crater zebras grazing during such nights with three well spaced rest periods of about an hour. Almost always one animal in a family group remains standing while the others sleep. They sleep heavily and sometimes need to be woken by a nudge from a fellow.

In some areas they drink just after nightfall, an operation which is attended by much noise as the animals have to keep in touch with one another acoustically. When many groups converge on a waterhole at night the noise can be tremendous. The call is most frequent in stallions and is made up of a series of explosive braying barks sometimes interspersed with a donkey-like catch of breath. The calls are uttered in various combinations like the neighing of domestic horses so that an individual can be recognized by its call. The importance of a recognizable call seems to be two-fold. It helps family groups to keep together and it identifies stallions. The latter is an important function because the males are potentially antagonistic so that social congregations depend upon the stallions resolving their aggression. Stallions very often call to one another and then approach slowly until they are able to touch noses. After cautious sniffing they then assume a reverse parallel position and sniff one another's genitals, then they stand side by side or lean against one another and with forehead, neck or shoulder rub up against one another with a measured up-and-down movement or else they nod their heads often pausing with chins on one another's shoulders. After further tentative sniffing they sometimes make an abrupt gesture or may even leap away as if threatened and a fight may follow but such encounters are more frequently without any sign of aggression and the animals may stand still in clumps for long periods.

Sometimes several stallions join in a mutual rubbing session, each jostling for a place; Antonius (1951) described such behaviour in confined zebras centering on a dung deposit to which each male contributed his own dung and urine after smelling and lip curling. Challenges between two male horses *E. caballus* sometimes involve deviation by one or both stallions to a dung pile where smelling, defaecating and smelling precede a high-stepping, arched-neck approach followed by mutual sniffing, squealing and generally some rearing and striking out with the hooves interspersed with neck or shoulder pushing contests and outright fighting. Feral stallions may return to a dung pile and defaecate several times during such confrontations (Feist, 1971) but the effect of such challenges is centrifugal in that the two animals break away from one another whereas up to six or seven common zebras may join in a


ears showing up in long grass

prolonged centripetal ceremony in which overt fighting is relatively rare. Although the common zebra stallions are clearly attracted to one another there is often an undercurrent of tension and occasionally snapping and fighting break out. Verheyen (1951) described approaching such a male group to film them (presumably in a vehicle). Suddenly almost all the members of the group threw themselves upon one another trying to bite necks or front legs. He interpreted this as redirected aggression but it is more likely that his interruption had precipitated the aggression which this stallion ceremony is designed to avoid or resolve. Klingel (1967) remarked that the ritual is mainly performed by males of matching size.

Antonius (1940) first described zebras making what he called "*rossichkeit-gesicht*", chewing with open mouth and a sort of grin; I consider this to be a vestige of grooming behaviour and have suggested that a uniquely zebrine bonding system has evolved (p. 134). Although common in all zebra meetings, Klingel found this expression most frequently directed by young males towards superiors or to strangers and interpreted it as a submissive gesture.

All-male groups are characteristic of this zebra and of the other zebra species and these gatherings number up to sixteen animals and can be of mixed ages, all subadult or sometimes all older animals including very elderly stallions that Klingel (1967) sometimes recognized as having recently left a family herd. The nucleus for a male group is often the attachment formed by a younger stallion following an older one. Klingel noted one such pair remaining together for over a year having both previously kept company with a female and her foals, and, in another case, a sick stallion parted from his family group with two of the young males of the group remaining with him. Apart from such attachments on the part of young animals, stallion groups have no stability of membership and they seem to be loose associations. Their members consist of immature and post-mature males. The only indications of rank seen by Klingel were denoted by the "follower" relationship and by subadults making the gesture of chewing *in vacuo*. It would seem that relationships are too tenuous and transitory for the assertion of a rank hierarchy but sociality is apparently enhanced and male aggression suppressed by these male rituals. However, male rivalry becomes intense and disruptive with the appearance of young females in oestrus and this is only resolved through the development of permanent attachment between a male and a female, itself the outcome of competition and continuous warding by the stallion. This association becomes the nucleus of the "family group", more females are collected by the more energetic males and larger groups can be taken over intact from an old, disabled or missing male. That unattached males are always on the look out for such an opportunity was well illustrated by Klingel (1967) when an immobilized stallion had his family group appropriated for the few hours he was under sedation.

If we consider the development of a male zebra, he is initially very closely attached to his mother, but the arrival of a new foal breaks the bonds and his continued tolerance within the group depends upon persistent submission to the family stallion or else he joins a bachelor group; with maturity at five or six years he seeks out females and eventually attaches himself to a female or small group of females and their young. A most important mechanism in the

development of this attachment is mutual grooming on the neck, shoulder and back.

Mutual grooming is very characteristic of foals and of course of the mare and her foal. Klingel found that mares seldom groomed one another and strangers never did. Nibbling can go on for as much as half an hour and can occur several times a day. It is sustained longest after a parting. Klingel found he could tame a captive wild zebra in two days, simply by persistent rubbing with a coarse brush. Once this attachment with a female or females is formed, the association is apparently reasonably permanent and Klingel (1967) has stressed that this is a closed group that is respected by other males.

The female zebra also started with close attachment to her mother but this too is loosened with the birth of another foal. Nevertheless she remains with the family and will stay on permanently if the stallion can prevent her abduction. The young female has her first oestrus at between thirteen to eighteen months, whereupon all the stallions in the neighbourhood, both bachelors and family stallions, try to drive her out of her group. Klingel (1964a) has pointed out that it is only young females that advertise their oestrus, standing with legs straddled, head lowered and tail raised. The oestrus of an adult mare within the family is instead only given away by scent, so that normally she is mated by her family stallion. That the stance of a subadult female subserves an important social mechanism is revealed by her refusal to allow copulation until she is at least eighteen months old (although she is infertile for yet another year), by which time she generally has a permanent liaison with a male. Klingel found only one case in forty-four of a filly remaining with the parent stallion. In cases where the filly joins an established family, Klingel observed that the other females are initially

hostile and that the new arrival assumes a low rank within the group in spite of her being closely attended by the male.

Within closed groups of zebras, female hierarchies develop. This comes into prominence on journeys, at which time the senior mare leads with her youngest foal at heel, each mare following in single file in order of precedence. The hierarchy is established by means of threats with the teeth or occasional kicks and Klingel saw changes in the peck order which might have been influenced by oestrus or pregnancy. No sick or old animal became or remained a leading mare. In any sort of alarm, or when concentrated on good grazing, zebras will form close clusters without discrimination. As soon as the stimuli bringing them together cease to operate, common zebras separate out again into family groups.

Zebra patterns have been compared to human finger prints and Klingel (1967) gives conclusive evidence that the members of a group identify one another primarily by sight, although the voice, which is equally individual, plays the decisive role in very large aggregations and on dark nights. It is interesting that many of the more highly developed social herbivores, such as elephants, buffaloes, elands and zebras should notice absentees from their group and search for them. All classes within a family group seek for one another except that the females do not search for other females nor for the older colts. The stallion is generally passively waited for or called to by the females but, in spite of the social group being the product of his behaviour a lost or ousted stallion is quickly replaced. By contrast, Klingel described several examples of young males leaving the family group after loss of the stallion and subsequently seeking him out.

The adult stallion is a tireless warden, searching out any lost or wayward member of the group, calling and searching until the lost one is found even amid congregated thousands of zebras and gnus. Family groups very frequently include members with disabilities of various sorts and these are always waited for if they lag, or defended and led back if they are attacked.

Zebras are capable of daring defences and rescues in the face of danger, Verheyen (1951) tells of approaching a wounded mare, whereupon a tightly clumped group of six zebras advanced at full gallop and surrounding the mare tried to move away with her. As he came up to put an end to her, the stallion suddenly tore up, touched the mare's muzzle and galloped straight at the advancing riflemen. Van Lawick (1970) recounted how zebras foiled a pack of wild dogs. After a chase the dogs isolated a mare with her foal and a yearling and brought them to bay, the dogs tried to grab the foal but were turned back by the mother or the yearling, neither of which left the foal unprotected from any direction. The foal remained close to its mother's side until the beleaguered trio were rescued by their family group of ten zebras which closed around the mother and her two offspring, wheeled round and galloped off in a closely packed group.

Approaching danger is often signalled by mares and stallions with a loud bark and they also snort when tense. Screams may be uttered by young animals that have been caught by an enemy and this may provoke a retaliation either in concert or from the stallion alone.

"A zebra stallion—with an open and bleeding sore on one flank—was being attacked by five hyaenas. The old stallion kicked out furiously as two hyaenas rushed in from behind. One of these received a blow on the head from a hoof, which dazed it for a while, and then it skulked off. The zebra—still kicking and bucking with head low and teeth bared—caught another hyaena by the loose skin on its back, and threw it twenty feet to the side. The others then sneakingly withdrew and the zebra rejoined the herd." (Cullen, 1969.)

The stallion's spirit must excite admiration, yet once firmly seized he may quietly allow himself to be dismembered and defensive behaviour seems to be most effective at the beginning of a chase. The deterrent effect would probably be still greater when several stallions are present. At night, when families usually rest close together, they clump at the approach of wild dogs or hyaenas and the stallions present a formidable rearguard. It is interesting that a stallion may behave no differently when accompanying a herd of elands (Vol. IIIC). The zebra's reaction to lions in their vicinity is generally to become very alert and stand in a semi-circle at about 100 m and never less than 50 m from the lions. Cheetahs and wild dogs are approached more closely and during daylight single hyaenas can come within a few metres of a zebra without exciting much interest. Occasionally stallions may try mock charges to drive lions off.

Zebras have been tested for speed and can run at 60—70 km per hour, yet Kruuk (1972) found that in two-thirds of his clocked hyaenas hunts they were running at less than 30 km per hour, a slowing down that is probably related to the group waiting for the defending stallion to catch up.

Apart from man, hyaenas and lions are the two major predators of zebras. In Ngorongoro and Serengeti the two carnivores kill different classes of animals. Hyaenas chase the herd until they can isolate an individual, usually a young one or a female. Kruuk (1972) found that half of the zebras that were preyed upon were less than four years old and more than two-thirds of hyaena kills were females. Kruuk observed that a stallion's determined rush right at the start of a hunt was sometimes enough to deter the hyaenas, but of all the hunts that he watched 31% were successful. In hunts after families lions were only successful in 21% of attempts observed by Schaller. In an aggregation of families the lion's chances of a meal improve but it is clear that the most vulnerable zebra to a lion is a solitary one (which is almost certain to be an old male), thus when lions hunted a single animal, Schaller (1972) found a 60% success rate. A sample of zebras shot in Serengeti at the time of Schaller's study suggested a preponderance of males in the population. There were more young females dying of diseases and malnutrition so that Schaller concluded the lions were killing the most available animals in the zebra population.

Because of the protective responses of the herd the loss of foals to predators is much lower than it is for species like gnus and hartebeest.

The fate of young animals will depend to a large extent on the rainfall pattern of the year. In the Nairobi area (Athi-Kapiti plains) Peterson and Casebeer (1972) estimated that the annual mortality of juveniles and newly born zebras might range between 30% and 60% while the average for adults

was about 17%. They found a slight preponderance of females and that fully adult animals comprised 60—70% of the population. In Ngorongoro, Klingel (1969c) found 48% of the previous year's offspring still with their mothers at the beginning of the following year. In Serengeti this figure dropped to 31% and in progressively drier parks in southern Africa the number of the foals declines in proportion with the rainfall so that at Etosha, on the edge of the Kalahari, fewer than 14% have been recorded surviving their first year.

Zebras have a single major birth peak and one foal is born each year after a gestation of about one year (361—390 days according to Wackernagel, 1964a). There is a *post partum* oestrus about one week after the foal is born. The rate of foaling is thought to be closely correlated with rainfall and range conditions of the previous year. In northern Tanzania, about two-thirds of all births occur during the rainy months of January—March (Klingel, 1969c).

Mating within a family group is the prerogative of the stallion. Considering the general excitement that fillies in oestrus cause this exclusiveness is surprising. However, knowledge of her oestrus is generally concealed because the adult mare does not alter her posture while in oestrus, so that her condition can only be detected by sampling her urine. Zebra stallions raise their head in *flehmen* and sometimes trot with their noses thrown to the sky and their lips curled back. Both wild and captive stallions will cover the female's excreta with their own, a function which Trumler (1958) suggests has the purpose of obscuring the mare's scent. As Klingel points out, the habit may derive from territorial behaviour but obliteration of the female's scent may help maintain the integrity of the family unit. Although strange males, normally showed no interest in the mature family mares, Klingel discovered that his immobilizing drug (M 99 and Hyoscin) caused animals to stand on widely straddled legs with their tails raised, which is the oestrus posture of the young mare. When he drugged a mare every stallion in sight converged on her and fierce fighting immediately broke out. Some males mounted the drugged mare but all interest in her was lost as soon as she resumed a normal position.

cantering while flehming

A female is generally competed for and annexed before she is sexually mature. At some time between the ages of one and two years the young female will suddenly assume an exaggerated and prolonged oestrus posture but at the same time she repulses all attempts at copulation and when the stallions converge on the group she keeps with the others while they clump defensively. Eventually, the efforts of all the stallions (Klingel counted 18 in one instance) succeed in isolating her.

y ♀ in oestrus

> "The young mare normally does not stay with the stallion which abducts her. When she has been separated from her original family the fight over her continues and only ceases when oestrus ends. With the next oestrus it starts all over again up to the age of 2 to 2½ years, when the mare becomes a permanent member of a family. Should the stallion, which is ultimately successful be a family stallion, he increases the number of mares in his unit and apart from the very rare incidents of adult mares getting lost and then being taken into another family, this is the only way that families add to their number of adult mares. Should the stallion be a bachelor he forms the nucleus of a new family with this mare." (Klingel, 1969c.)

Zebras usually fight only over young females. Fights may begin with circling in which the opponents may find themselves in the reverse parallel position in which case they tend to go for one another's back legs (some observers believe they are attempting to castrate one another!) upon which both drop onto their carpal joints and continue trying to bite one another on the legs. Alternatively, a neck contest may develop in which the animals cross their necks and each strains either up or down. The teeth are not used at first but as the intensity of the contest increases one or other may snap and this may lead to a rearing fight in which both animals flail at each other with their forelegs and bite hard. The fight usually ends with one turning tail, throwing a few kicks with his hind legs to keep off his pursuer.

Courtship lasts throughout the mare's oestrus; mounting is often preceded by the male nibbling the female's shoulder, neck and body. However, successful copulation is only achieved at the height of her oestrus. The mare

can delay parturition if she is disturbed and she generally gives birth lying on her side. The male is usually close by and very alert over the birth period. Captive stallions give away an impending birth by their excited whinnying. Young males weigh 33·3 kg at birth, females 31·5 kg (Wackernagel, 1964). Within a quarter of an hour the foal is on its legs and at one hour it may start to suck.

> "During the first few days after foaling, the mare, in a threatening posture, chases all other members of the group as well as any other zebras approaching within about 3 m of the foal. She even attacks the stallion, which is the alpha animal of the group. This behaviour is obviously correlated with the critical period of imprinting of the mother's image on the foal. New born foals follow any object near to them during the first days of life. The aggressive behaviour of the mare thus prevents the foal from accepting another animal as its mother. Several days later this behaviour of the mare ceases and all members of the group can contact the foal which by then seems to recognise its mother by her stripe pattern, voice and scent." (Klingel, 1969c.)

By the age of one week the foal has begun to eat grass and growth during the first two months is very rapid with gain averages of half a kilogram a day during this period.

The foals are very playful, chasing and racing one another and even other species of animals. Male foals indulge in mock fights.

Zebras associate with various species (see p. 141) and will share water or grazing with most other herbivores. Horned species larger than the zebra tend to be dominant. Temporary mixed herds of the two zebra species form in their area an overlap and one group in Tanzania was led by a feral donkey. Stallions sometimes attach themselves to herds of eland or buffalo.

Zebra suffer from several diseases including babeesia and anthrax. Schaller (1972) reported more females dying of disease than males on Serengeti, making it likely that a disproportionate segment of the Serengeti zebras were old males. Parasites include several species of tapeworm, botflies, the

lungworm *Dictyocaulus*, the bloodworm *Strongylus vulgaris* and *Parascaris* roundworms.

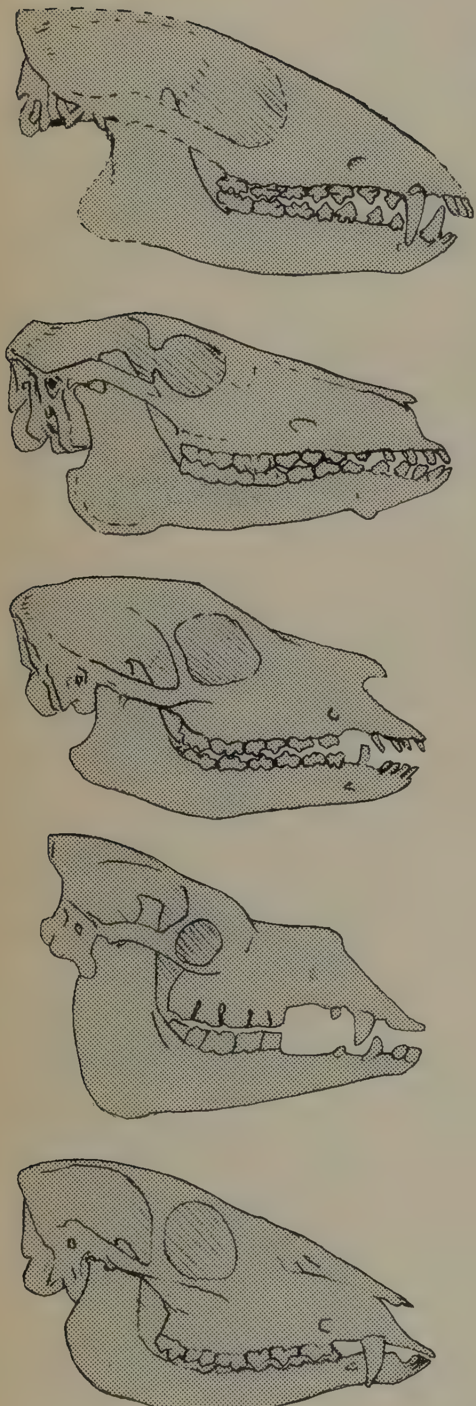
The population dynamics and productivity of the zebra has been investigated with a view to managing and cropping them (Peterson and Casebeer, 1972; Skoog and Gogan, 1975; Bindernagel, 1975).

Before the arrival of motorcars in Kenya efforts were made to put zebras into saddle and harness, partly out of caprice and partly in regret that so beautiful an animal should be condemned as useless vermin.

For the Karamojong the zebra symbolizes one of the four generation sets. In their dances the women paint themselves with black and white stripes, try to walk, jump and even turn their heads like zebras in imitation of their beauty and vitality. In Singida, where zebras no longer survive, the Wanyaturu regarded the zebra as the supreme symbol of beauty and fruitfulness.

Artiodactyls

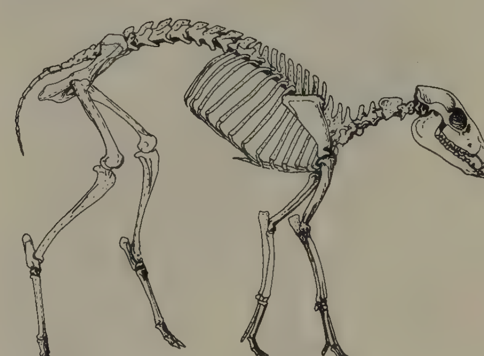
Artiodactyla



The development of a diastema in primitive artiodactyls *Homacodon* (Eocene); *Poëbrotherium* (Oligocene); *Archaeomeryx* (Eocene); *Camelus*; *Hyemoschus.*

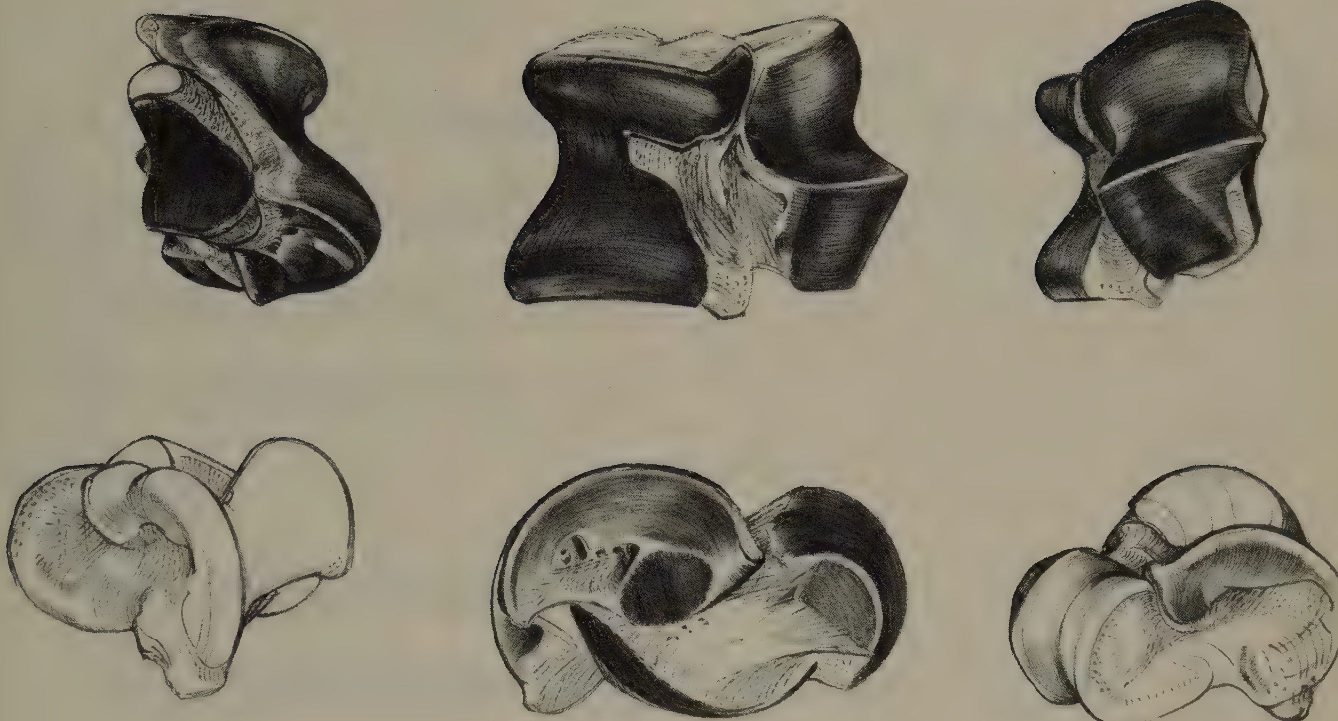
It has been one of the intentions of this book to assert that the living fauna of East Africa exemplifies the evolutionary process at a variety of different levels.

The artiodactyls described in this and the following volume illustrate the progress of one of the most important mammal lineages. The first artiodactyls were not very distant from carnivores, had prominent canine teeth and an omnivorous diet. This stage of the group's evolution is poorly known in the fossil record but the living bushpig is a useful aid to our imagination of this crucial transition between carnivorous and herbivorous diets. Likewise, the chevrotain takes us a stage further towards the horned antelopes and oxen and its four-toed legs are intermediate in several respects between those of primitive pigs and advanced antelopes with their elongated and fused metapodials. (Actually a particularly apt illustration of artiodactyl evolution is provided by a peculiar extinct traguloid, *Leptomeryx*, which has four toes on its very short front legs and two on its long hindlegs showing very simply that unnecessary bones are lost as limbs become longer.)



The primitive horned bovids are typified by duikers or pigmy antelopes and these are described with more advanced bovids in the next part of this volume.

Special offshoots from the main line of artiodactyl progressive evolution are no less interesting and the hippopotamus, warthog and giraffe are all extreme end-products of eccentric adaptation with unusual diets or strategies for survival. They are all very successful species and it is significant that less specialized relatives, the pigmy hippopotamus, the giant hog and the okapi are rarer and have much more restricted ranges.



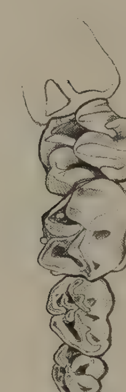
Artiodactyls are distinguished by their even toes with the axis passing between the third and fourth digits, the two toes that bear the weight in all types.

In advanced artiodactyls the metapodials fuse to form a canon bone and this is part of a general loss of versatility in limb movement but an improvement in efficient fore-aft leverage. For example, the lower end of the tibia hinges on the lower leg by sliding along a deeply grooved arc in the upper surface of the astragalus. There are similar limitations on play at the front end of the astragalus and the four articular surfaces of this beautifully functional pivot give a characteristically artiodactyl sculpture to the bone.

In most cases the skulls of living artiodactyls have been adapted to highly specific modes of combat requiring elaboration of canines, incisors or horns. The molars instead do illustrate a progression from the bushpigs' primitive condition of strong champing teeth with thick enamel cusps to the advanced bovids with shearing hypsodont teeth. The cheek teeth of a young giraffe illustrate how wear on crescent-shaped cusps can produce a zig-zag pattern of sharp enamel margins around dentine valleys, a surface well suited to the cutting up and fine grinding of vegetation. Both chevrotain and giraffe, which are browsers, have relatively low-crowned teeth.

The adaptation of artiodactyls to grazing is primarily a bovid success story and is discussed in Volume IIIC.

The separation of function between the incisors and cheek teeth and lengthening of the face has meant the development of a diastema in most species and the majority have reduced the front dentition of the upper jaw.



Above: Astragalus of extinct *Hippopotamus* sp.
Margin: Cheek teeth of young giraffe.

The increasing complexity of artiodactyl stomachs.

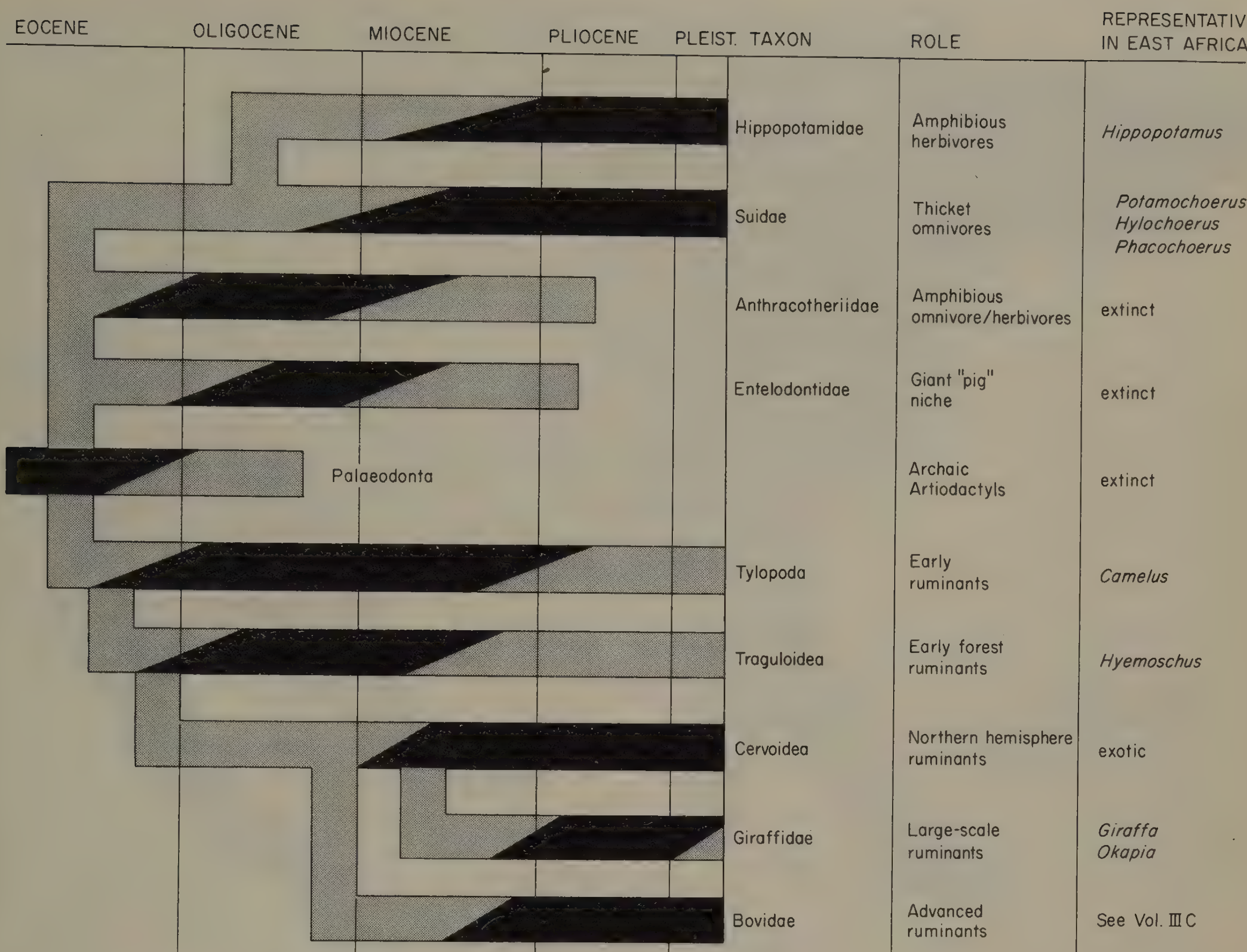
Ruminants usually rest while chewing the cud which is of great significance in their activity cycles. They are passive except for a moving jaw and bulging cheeks and if the chin is brightly coloured or patterned this movement can be conspicuous. Facial pattern may be influenced by such considerations, for example the okapi has a dark chin but some species of duiker have a sharp tonal contrast which apparently advertises the movement.

Finally, the most significant feature of artiodactyl evolution is the progressive improvement of their digestion by a system of storing, rechewing and sifting of the food and a remarkable symbiosis with bacteria and protozoa living within the chambers of the stomach. These break down cellulose and release nutrients.

All other herbivores are inferior in the efficiency of their digestion and the success of artiodactyls can be attributed to this major innovation.

The ruminants probably gain their greatest advantage in nitrogen cycling and in conservation of urea. Fermentation of dietary protein releases ammonia which is absorbed and converted to urea in the liver. Urea is cycled back through the blood system and parotid gland and both urea and ammonia are used as a source of protein by bacteria in the rumen. The bacteria pass into the abomasum where they are in turn digested by proteases. By cycling urea rather than excreting it the ruminant is able to use all available nitrogen, save urinary water and perhaps protect itself from amino-acid imbalance (Janis, 1976).

A diversity of social and ecological adaptation in the non-bovid artiodactyls is discussed in the following profiles.



Tentative scheme for radiation of artiodactyls. Abundant or dominant species in fossil record.

Chewing the cud. Jaw movements and the use of the cheeks in *Giraffa* (from film).

Pigs

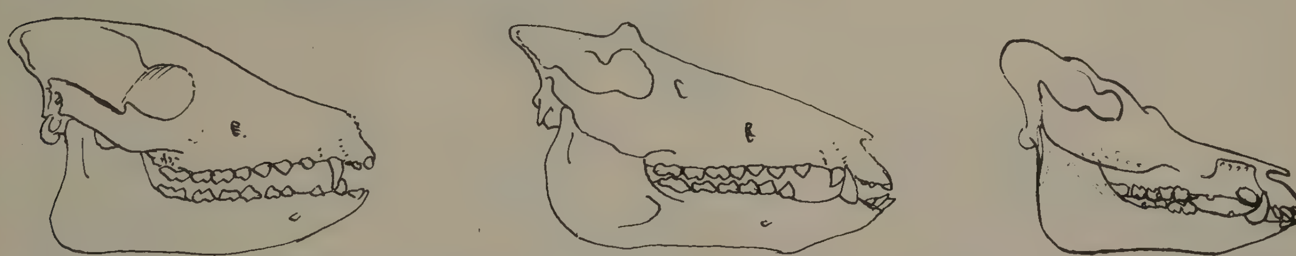
Suidae

Pigs occur in most of the important African fossil sites and their significance for chronology has been widely recognized. Interpreting the functional and comparative anatomy of pigs in terms of ecological adaptation is equally important for a broader understanding of Plio-Pleistocene ecology and the African suids should be examined with this in mind.

During the earliest phases of an ecological radiation by the archaic even-toed ungulates one branch adapted to a foraging existence in which an omnivorous diet was allied with a robust and compact body build.

At an advantage in thick vegetation and swampy forests, these animals would have been able to penetrate difficult habitats and eat the stems, shoots and roots of the dense undergrowth in addition to invertebrates and various smaller and less active types of vertebrates.

A generalized dentition, wedge-shaped skull, tough skin and relatively short legs have been retained by most of the modern descendants of these early suids and in some respects the African bushpig, *Potamochoerus*, can conveniently exemplify the archetypal pig. It has a nearly complete and relatively unspecialized dentition but eats a high proportion of roots which are unearthed by its tubular snout and sharp-edged nasal disc with incidental help from the small canines. It has an acute sense of smell and lives in wooded habitats retiring into the densest thickets to sleep. The occupation of this niche by the bushpig is virtually unchallenged today and the species is widely distributed wherever there are forests, woods or thickets and moderately moist soils. However in spite of the absence of any significant overlap in diet the bushpig is very rare in areas where the giant hog is abundant and I believe this may be due to the latter monopolizing all suitable shelter. There appears to be less incompatability between warthogs and giant hog populations in spite of both being grazers and this may be because they have different requirements for shelter (see pp. 216, 234).



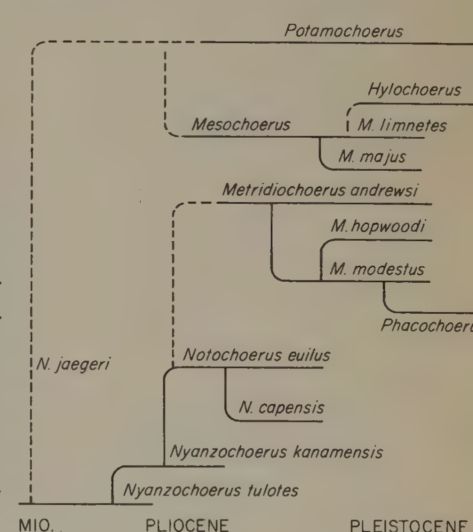
Left: *Palaeochoerus* (Oligocene); centre: *Bunolistriodon* (Eurasian Miocene); right: *Nyanzochoerus tulotes* (African Miocene).

In this connexion it is interesting that *Potamochoerus* should suddenly appear in Mid-Pliocene deposits at Laetolil after which it effectively disappears from the fossil record, apparently superseded by the giant hog's ancestral stock, *Mesochoerus* and the phachoerine *Metridochoerus* (White and Harris, 1977).

The common ancestor of the three African species was probably a Miocene pig somewhat intermediate between *Bunolistriodon* and *Nyanzochoerus* and this primary radiation might have occurred in Eurasia.

The most recent study of pig phylogeny by White and Harris (1977) has recognized four distinct lineages in the African Mid-Pliocene. *Potamochoerus* as a primitive *Sus*-like pig may have come into Africa from Eurasia at about this time. *Mesochoerus limnetes*, the immediate precursor of *Hylochoerus* also makes its first sudden appearance shortly after. White and Harris derive *Phacochoerus* from a third lineage, *Metridiochoerus*, and they note that between them *Metridiochoerus* and *Mesochoerus* eclipse the formerly dominant line of African pigs *Nyanzochoerus* and *Notochoerus*. *Metridiochoerus* may be of African origin but the nature of its connexion with *Nyanzochoerus* is not clear at present. However, in the discussion that follows I have assumed that there is some sort of phylogenetic link between *Nyanzochoerus–Notochoerus* and the *Metridiochoerus–Phacochoerus* lines and make comparisons between the contemporary *Phacochoerus* and *Notochoerus* to illustrate the nature of those gross changes in skull architecture that have undoubtedly taken place.

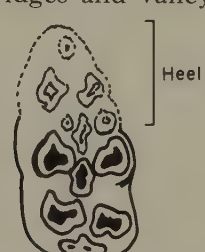
Below: Phylogeny of African pigs. (Modified after White and Harris, 1977.)



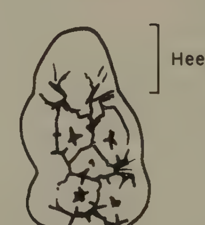
The enormous differences that exist today between bushpigs and giant hogs were not so marked in the Pliocene and there is an interesting *Mesochoerus* skull from Koobi Fora which shows that the two lines were not so far removed at that time.

The giant hog, *Hylochoerus*, has the general appearance of a typical pig and is also dependent on dense thickets for shelter. However, this species has a huge bulbous rhinarium which is quite unsuited and is scarcely ever used for rootling. Instead this pig relies on its broad mouth and lips to crop grass and lush herbaceous growth near the forest edge, in glades and along river courses. Reliance on grass in the diet is reflected in the more specialized structure of the teeth, particularly in the form of the third molar. In this

tooth the enamel pillars of the crown have been augmented behind by extra pillars which form a heel. Unlike the thick enamel cones of *Potamochoerus*, *Hylochoerus*' cusps are higher crowned and have thinner dentine and enamel but they are spaced out within a thick matrix of cement (which is altogether absent in the bushpig). Wear produces sharp ridges and these provide a milling surface but the cusps remain prominent and cut into the softer cement of the occluding tooth to produce a highly characteristic series of transverse ridges and valleys.



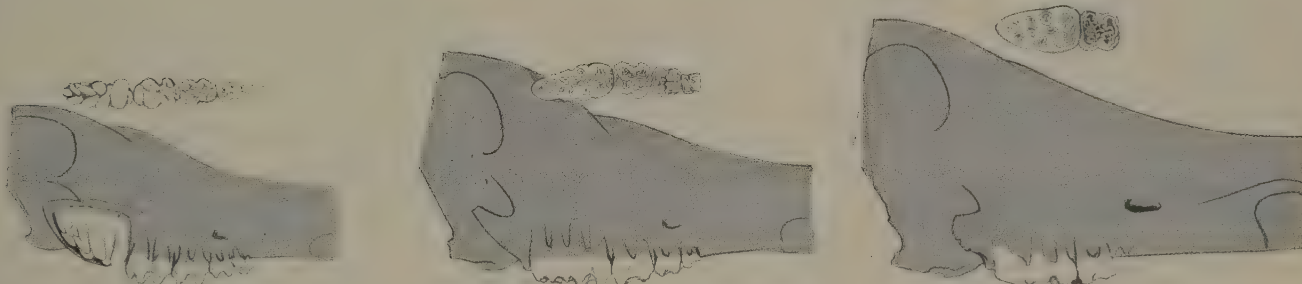
M^3
Hylochoerus



M^3
Potamochoerus

Instead of simply champing its jaws like *Potamochoerus*, mastication is achieved by swinging the jaw from side to side but the mandibular condyles have very little lateral play so the occluding teeth do not simply grate from side to side but traverse over a rather short radial course. This means that there is more movement at the front end of the toothrow than the back, which leads to early wear and attrition of the premolars. In any event, teeth that have fore-aft elongation and shallow roots are ill-suited to withstand such transverse stresses, let alone perform any masticatory function.

In the course of their development the molars of a growing hog are actually modified to accommodate to this type of mastication, suggesting that the mechanism is phylogenetically a relatively late makeshift. M_1 and M_2 are in use by the time a piglet is weaned, at which time they are narrow, deeply cusped and virtually without cement. M_3 develops at the back of the jaws, moves forward and pushes the toothrows forward. After the emergence of the upper M_3 an unusually long capsule remains collapsed and empty at the back of the maxilla. In the juvenile hog M_3 emerges as a long narrow tooth in which the pillars are already invested in cement but their general alignment is longitudinal and the eight to ten pillars of the heel double the length of the tooth. Subsequently the lengths of the teeth are not increased but all the molars expand in width as they augment their cement. As the upper third molar comes into occlusion and becomes worn the pillars appear to increase their transverse or lateral alignment. Development in the heel of this tooth seems to be minimal. The crown instead becomes the broadest and most important grinding surface but M_2 also becomes a broad and massive tooth (see drawings). To compensate for the inefficiency of its molars the young



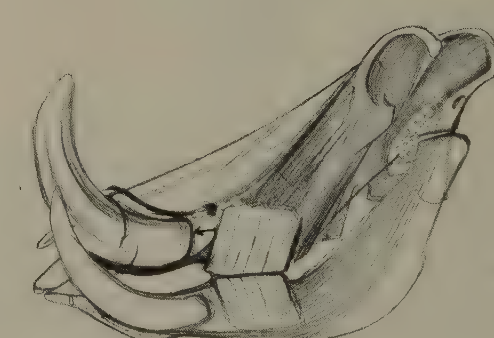
Toothwear and tooth succession in *Hylochoerus*. Juvenile, subadult and old, all female. Note the early loss of cusps, particularly at front end of tooth row.

hog selects softer food than the adult and grass in the dung of young *Hylochoerus* is relatively poorly masticated (see p. 214).

Lateral movements of the jaws are primarily operated by the pterygoid muscles which are exceptionally well developed in *Hylochoerus*, take origin from a greatly expanded pterygoid and insert on to the widely flared angles of the mandible, the outer margin of which develops a pronounced crenellated crest, attesting to the importance of this muscle. The *temporalis* muscle has correspondingly declined in both *Hylochoerus* and *Phacochoerus*, as was pointed out by Ewer (1970) in her detailed description of the cranial anatomy. The significance of these peculiarities for grosser aspects of skull architecture will be discussed later but it is clear that the giant hog has made extensive, if cumbersome adaptations to a herbivorous existence.

Because *Hylochoerus* requires a year round abundance of green fodder at ground level it is not found in areas of poorly distributed or unreliable rainfall and it is rare or absent in closed canopy forest. Its dependence on dense vegetation for shelter confines it to the vicinity of forests and thickets (but these may be mere galleries or relicts). These hogs sometimes chase off other herbivores from choice pastures but in spite of such functional intolerance it is only in areas of seasonal stability and great primary productivity that a herbivorous pig can hope to compete for the same resources with advanced ungulates. In habitats with abundant cover for predators their defensive behaviour (see p. 224) might favour giant hogs *vis-à-vis* other herbivores. The restriction of this species to forest-grassland mosaics within the equatorial region is partly explained by these limitations.

On the face of it grasslands and open woodlands should be inimical to pigs because soils are hard and there is not much bush to shelter in, while a great variety of fleet-footed and specially adapted bovids are formidable competitors when grass becomes scarce in the dry season. However, pigs are exceptionally well represented in the fossil record and the warthog *Phacochoerus* is but the last survivor of a variety of other grazing pigs that are now extinct (see the table, p. 185). Unlike *Hylochoerus* these pigs retained the ability to rootle as well as graze, and the key to their success is likely to have been an ability to turn to grass roots, rhizomes and leaf bases whenever surface feeding became difficult. In this way they avoided competition with the bovids at times when this might have become critical to survival. The need that pigs have for a secure shelter is met in the case of the warthog by the use of *Orycteropus* burrows and various natural caves and crevices (see p. 234). The ecological preferences of the three living pigs are indicated (opposite) for an area in western Uganda where their ranges overlap fairly extensively. Estimates of relative density were impossible to obtain and all pigs in the Siba area were hunted more intensively than elsewhere. However, direct observation of the animals and their traces together with consultation with local hunters, forestry and game department personnel and research workers helped to define the margins of each species' area of dominance.

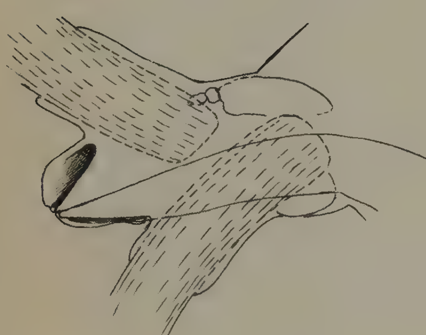


Adaptation to coarse grass grazing is manifested in *Phacochoerus* and various extinct pigs by the acquisition of very high crowned molars, the last of which, M_3, has extended the heel to such an extent that the tooth has tripled in length. Continuous growth at the back and slower growth at the front causes

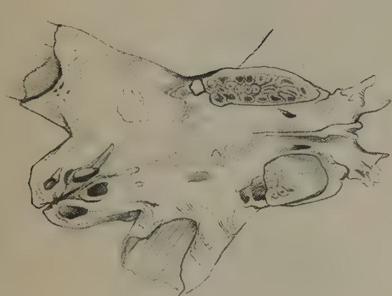
Ecological separation of three species of Suidae in Budongo Forest region.

the columns of the tooth to become progressively more oblique. The warthog sheds its three premolars at a relatively early age and finally loses its anterior two molars, so that the jaws of aged animals are filled by a single molar on each side (see drawings on previous page).

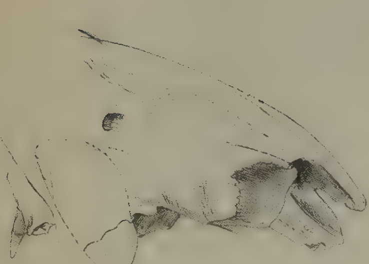
It seems that normal development of this tooth depends upon its forward traverse being unimpeded. The effect of a broken mandible obstructing tooth development in the upper jaw is illustrated (below) with the muzzle of an aged male warthog. After the fractures (which had probably been in at least two places and which had displaced the lower third molar on the right side so that it tilted upwards and inwards) normal occlusion became impossible



Probable explanation for aberrant M^3 and slewed growth of skull.



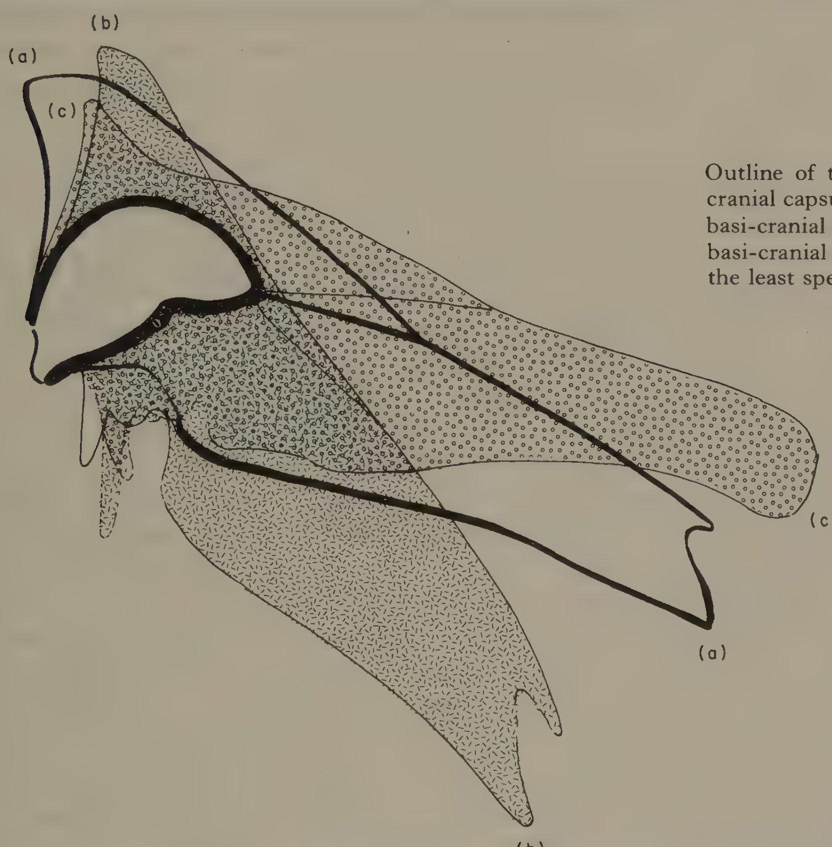
and the front end of the upper third molar met an opposing force exerted by the displaced lower molar. Instead of the enamel columns neatly progressing down a longitudinal axis in three rows they appear to have piled up in a cluster which became embedded in thick cement and acquired an almost tusk-like form. The accident must have occurred during an early stage in the tooth's development and before the skull had reached its maximum dimensions. The tooth and muzzle were able to progress forward unimpeded on the left half of the skull while growth was opposed on the right hand side by the lower molar. This not only distorted the upper molar but forced up the palate and held back the onward progress of the maxilla so that the whole skull slewed round the point of obstruction (see drawings).



This curious accident betrays that the area between the third molar and the tusk is vulnerable to distortion and it illustrates that ontogenetic growth of a tooth is an integral part of total skull development. It is also a reminder that teeth should not be considered in isolation from their cranial matrix. In earlier volumes I have pointed out phylogenetic parallels to ontogenetic accidents (Volume I, pp. 3—4; Volume II, p. 681) and suggested that in the course of evolution, displacements, enlargements or shrinkage of functional units tend to leave their mark in buckling or distortion of bones and sutures along areas of junction (Volume I, pp. 141, 147; Volume II, pp. 572—574).

The acquisition of a long shearing surface and extreme hyposodonty in *Phacochoerus* was achieved by multiplication and elongation of columns in

the heel of a single tooth, the third molar. Some hypsodonty is perceptible in a late Miocene pig, *Nyanzochoerus jaegeri*, but the trend was greatly accelerated in the Pliocene *Notochoerus* and *Metridiochoerus* and reached its maximum development in the Pleistocene phacochoerine pigs. Notochoerine and phacochoerine pigs developed heavy tusk sheaths at the front of the maxilla, while gross enlargement of a single molar involved a very considerable expansion of its bony bed at the back of the maxilla without comparable development in the medial zone. Indeed, the diminished roots and progressive loss of premolars and anterior molars in the warthog contracted the intervening area considerably, depressed the barrel of the snout and brought the roots of the canines close to the leading edges of the third molars. Comparing the medially sectioned skulls of *Phacochoerus* and *Potamochoerus* (the latter as a more conservative suid) the floors of the cranial capsules have a similar relationship to the occipital condyle but there is a downward flexure of the warthog's snout that takes place near the front of the brain (see figure of superimposed skull outlines below).



Outline of the skulls of three pigs in relation to the cranial capsule showing the bending downwards of the basi-cranial axis in *Phacochoerus* (b) and lifting of the basi-cranial axis in *Hylochoerus* (c), *Potamochoerus* (a) is the least specialized form.

Depression of the snout and progressive tooth reduction bring the warthog's functional molars closer to the front of the mouth yet the warthog's skull retains long-headed, typically suid proportions. This is due to an elongation between the tooth row and the squamosal which is not only due to the lengthened crown of M_3 but can be correlated with the mandibular condyle needing to rise well above the plane of occlusion, an arrangement that is typical of all mammals with mill-like or shearing dentition (Ewer, 1958a).

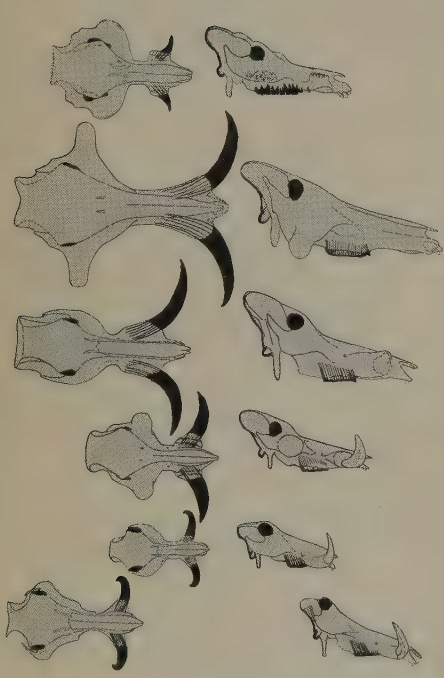
This region was equally elongated in *Notochoerus capensis*, which had already developed strongly hypsodont teeth of phacochoerine type by the Pliocene. However, this giant pig had long tusks which faced forwards; deep roots down the maxilla extended the muzzle and created a long narrow diastema between the cropping mouth and the molars.

In the living animal dense connective tissue must have capped and still further enlarged prominent bony projections on the zygomatic plate. These clearly served as protective guards or buffers during tusk contests.

The warthog exhibits vestigial projections at the jugal-squamosal symphysis and these underlie the largest of the facial "warts". While performing an important protective function the disproportionate size of this tissue may also reflect the warthog's giant ancestry; (*Potamochoerus* and *Hylochoerus* also seem to derive from larger ancestral types).

The deeply-rooted canines of *Notochoerus* must have reinforced the muzzle and might have provided a sound base for countering and delivering blows and thrusts but fighting was probably clumsy and the long tusk arches must have hampered feeding. A more lateral orientation and an increase in the upward curl of the tusks would reduce interference and allow more versatile feeding but such alterations would substantially shorten the snout and alter the dynamics of tusk clashing quite fundamentally.

A heavy investment of bone and even the surface texture of the warthog's tusk sheaths are consistent with the tusks having freed themselves from the barrel of the muzzle and swung out sideways, curling upwards and back.



Nyanzochoerus tulotes (Miocene); *Notochoerus capensis* (Pliocene); *Metridiochoerus andrewsi* (Pliocene); *Metridiochoerus jacksoni* (Pleistocene); *Phacochoerus antiquus* (Pleistocene); *Phacochoerus africanus* (Holocene).

The tusks are the largest and heaviest of any living pig and because they are carried at the end of a long skull their employment as weapons or shields requires that leverage from the upper neck muscles be exerted as high as possible above the occipital condylar pivot. Furthermore, downward flexure at the snout needs the lever of the occiput to be brought forward as far as possible. As can be seen from the superimposed outlines of skulls (p. 191). *Phacochoerus* has a high occipital crest angled forward so that the profile of forehead and snout remains straight. This is a late innovation in *P. aethiopicus* because the occiput was more backward and depressed in the mid-Pleistocene *P. antiquus*.

The latter fossil also demonstrates that elevation of occiput, zygomatic plate, squamosal and orbit has been a wholesale movement which improves both occipital and mandibular leverage at the same time as raising the cheek bones and their associated warts. Perhaps this uplift of the facial "shield" matches the higher curve of the tusks. Greater prominence for the eyes might be related both to more open but grassy environments and to overlooking the tusks. In any event, the eyes are exceptionally important in tests of dominance and the contestants watch one another continuously.

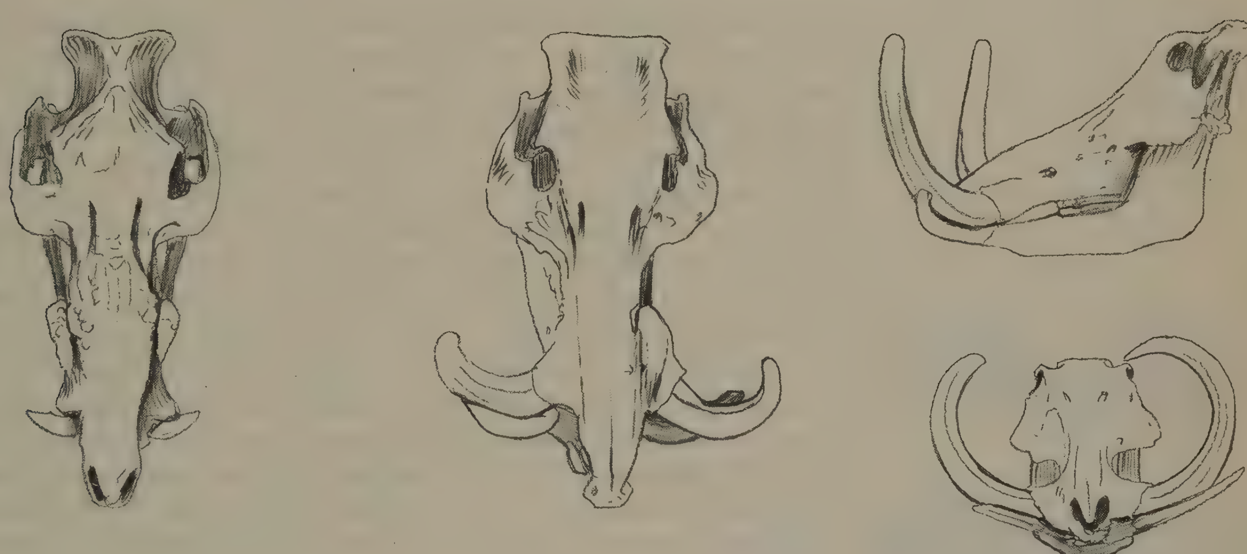
The use of the tusks in fights is illustrated on p. 233. The preliminaries may include mutual snout sniffing and a parade in which profile views in the "proud" position are presented. The first engagements of the tusks may be on the knees or standing and there is much see-sawing of the engaged heads as the pigs test their strength and heads may be brought into opposition.

From time to time this frontal sparring is interrupted by an extremely rapid disengagement by one pig followed by a sideways strike in which the head and neck twist over 90 degrees or more so that the force of the blow

comes from both tusks. If the other pig fails to match the blow with a parrying twist it is likely to be thrown off balance and the advantage is followed up by the first pig tusking at the exposed shoulder or body. If the side of the head is exposed there is the danger of a jaw being broken (in spite of the ridge of thick tissue that protects it) and I have noted healed fractures on several jaws I found.

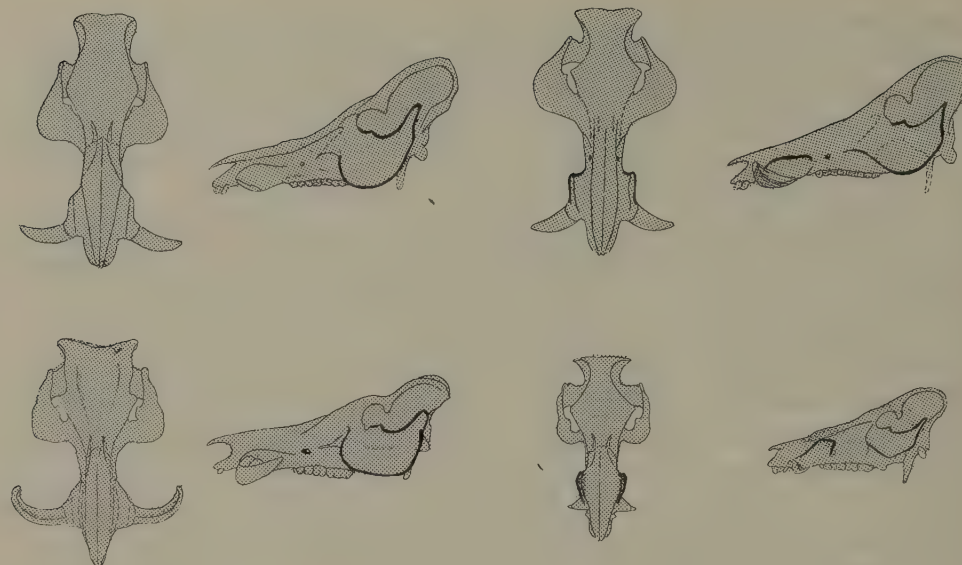
Tame captives can be provoked into some of these actions by boxing their snouts with a clenched fist and their sideways slams are extraordinarily fast and forceful, even in very young piglets; rapid sidelong flips are sometimes made *in vacuo* during juvenile games. When a lateral blow is delivered during the highest intensity of an adult male contest the entire forequarters may be thrown over sideways to give added weight and force. At such times the antagonists wheel and spar at great speed and the momentum of a clash may be increased by a short rush.

Of the living African pigs only the warthog's tusks project sufficiently for them to be used for direct engagement. Their elevation above the plane of the snout allows forms of tusk wrestling or fencing and the tusks alternatively deliver and absorb the impact of blows.



Left: *Potamochoerus*; centre: *Hylochoerus*; right: *Phacochoerus*.

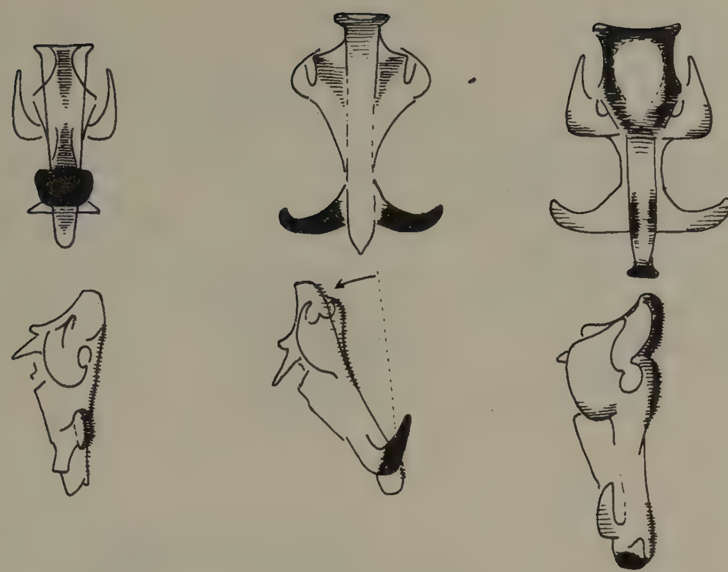
Because they point sideways at a low angle the smaller tusks of bushpigs and giant hogs can only be used singly during lateral swings and, being rooted further back in the skull, they have less leverage. The bushpig's sharp tusks are particularly short and contestants spar with their long narrow snouts in such a way that they fence off stabs or slashes. This fencing has become ritualized and in adapting to this their skull has been modified.



Top row: *Mesochoerus limnetes* from Koobi Fora; (left) "normal" type from upper members; (right) type resembling bushpig from lower member.
Bottom row: (left) *Hylochoerus*; (right) *Potamochoerus*.

I have already mentioned a *Mesochoerus* skull from Koobi Fora that combines hylochoerine and potamochoerine features. This was a large pig with inflated zygomatic arches and canine roots that were aligned alongside rather than being incorporated within the barrel of the snout. Large cheek shields can only encumber rapid manoeuvre of the snout, particularly if they extend forward of the orbit and in *Potamochoerus* they have retreated above the very back of the toothrow. Instead, a protective device has developed further forward from a bony flange that covers the sheath of the canine in *Mesochoerus*. This excrescence rises behind the arc of the tusk and prohibits any possibility that the muscles or tendons serving the snout might get cut during a fight. The elevated rugose surface of this flange is aligned beside a matching rugosity on the muzzle and the dense tissue that caps these prominences forms a complex of knobs half way down the snout. Down the midline there is a broad notch between the knobs and between them and the tusks and behind the rhinarium there are depressions which allow tilted heads to make various purchases. Weight and strength can thus be tested in relatively safe manner; Frädrich (in Grzimek, 1972) has described animals facing each other and opposing their foreheads with their noses and snouts crossed like swords. Pushing to and fro, they alternately use their snouts to box each other with vigorous butts. During the more dangerous sideways boxing or slashing contestants parry so that the area of contact is restricted to the middle or front of the muzzle, where the onslaught is more harmlessly absorbed. The tall occiput provides the leverage for rootling and snout boxing and it is this rather than a long purchase for the temporal muscles that influences height.

While the general architecture of the bushpig's skull and dentition remain very conservative it does seem that their diminished cheeks and peculiar nasal knobs are linked adaptations towards a highly specific fighting technique



Surfaces coming into contact with opponent during ritualized contests: (a) *Potamochoerus*; (b) *Phacochoerus*; (c) *Hylochoerus*.

which deserves further study. *Hylochoerus*, on the other hand, has retained tusks and zygomatic arches that remain similar both to *Mesochoerus* and to *Nyanzochoerus*. In fact, it is very likely that the major peculiarities of the giant hog's skull shape are traceable to relatively late changes in the dentition of a Pleistocene population of *Mesochoerus limnetes*.

In the late Pliocene *Mesochoerus* molars were already slightly taller and the talon larger than in the bushpig but the enamel was still very thick and with very little cement. During the Pleistocene *Mesochoerus* became a dominant suid genus and a chronological enlargement of the talon and simultaneous thinning of the enamel with increasing cement was first noticed by Coppens (Arambourg *et al.*, 1969) who broke down the Omo series into ancient, typical and progressive. Pleistocene *Mesochoerus* also increased the size of the pterygoid, a development that betrays greater lateral movement of the jaw but one that also involves wholesale movements within the skull which are relevant to understanding *Hylochoerus* cranial architecture. In primitive pigs the pterygoid muscles were shallow and originated from diminutive pterygoids and the area between the occipital condyle and the back of the tooth was short and confined so that when the role of the pterygoid muscles increased it was necessary not only for its insertions on the mandible to become broader and more splayed but more space had to be found for an enlarged origin of the pterygoid bone. A simultaneous widening of the mandibular angle and of the space immediately behind the toothrow can only lift the angle of the muzzle in relation to the basi-cranial axis. It is this elevation as well as the other differences that distinguish Pleistocene *Mesochoerus* from Pliocene forms and the muzzle is highest in *Hylochoerus*, where it can be correlated with a superficial pterygoid muscle that is almost as large as the masseter (see drawing). The branches of the lower mandible are also most widely splayed in *Hylochoerus*, suggesting that the trend towards

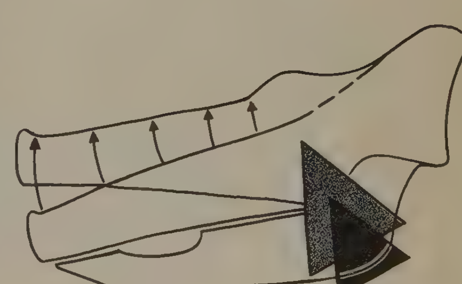
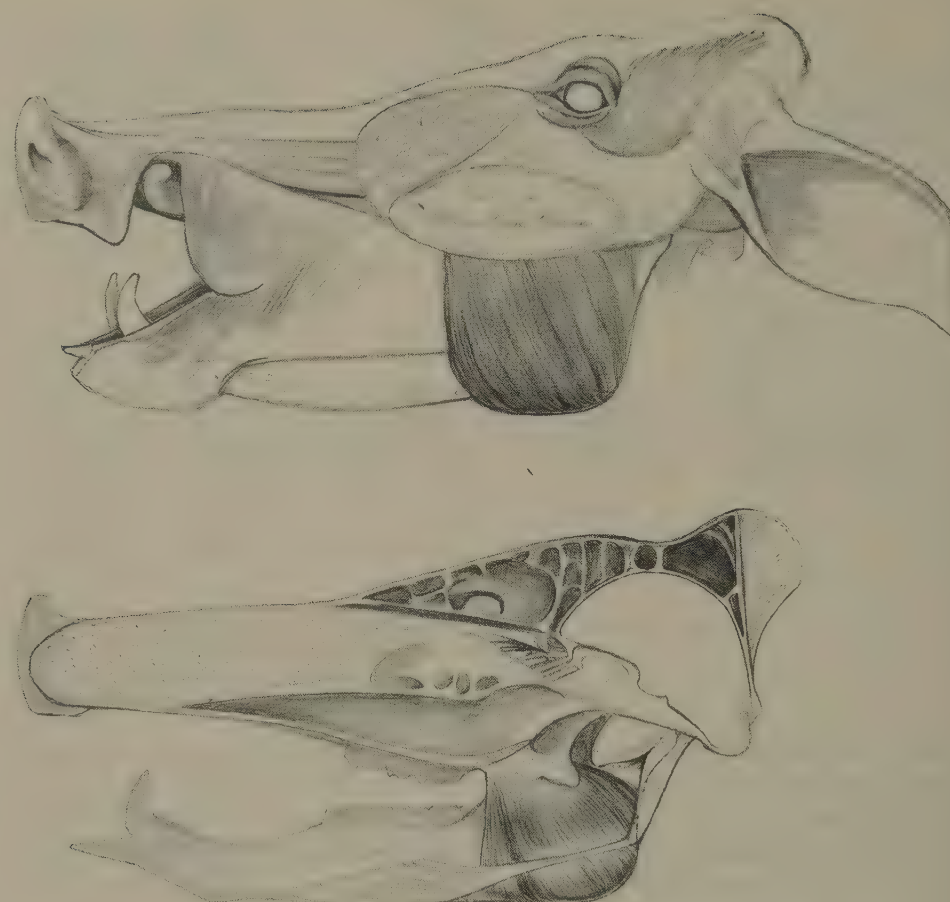


Diagram to demonstrate role of enlarging pterygoideus muscles as wedges opening up the base of the skull, lifting the muzzle and buckling the forehead.



Surface dissection (upper) and cross-section (lower) of male *Hylochoerus* for comparison of masseter and pterygoideus muscles.

lateral chewing has reached its most extreme development in the giant hog. Indeed by adopting an almost exclusively herbivorous diet the hylochoere lineage probably shifted out of the mesochoere niche since greater development of the nasal musculature implies a more functional rhinarium and greater versatility in the feeding habits of *Mesochoerus*.

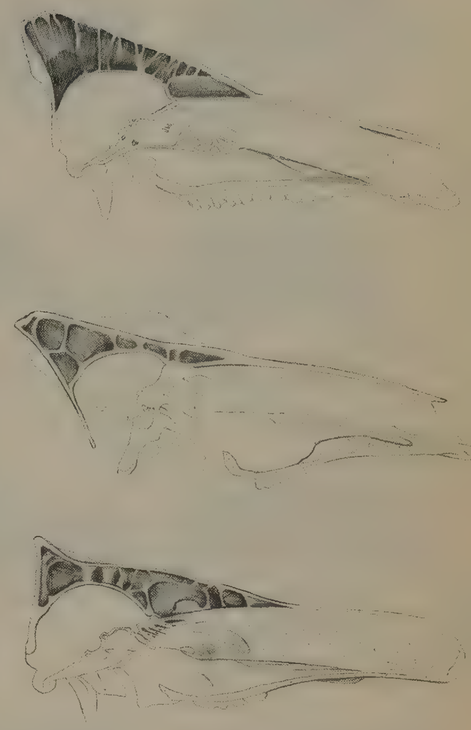
The faunal associations of the latter fossil imply relatively dry savanna habitats near water while its deeper crowns suggest an ability to cope with coarse grasses and perhaps grass roots. The extinction of *Mesochoerus* and survival of *Hylochoerus* illustrates that a species which is well adapted to a relatively narrow ecological niche may have long-term advantages in spite of an apparently inferior dentition and, in this case, a "makeshift" mode of mastication.

By discarding use of the rhinarium to excavate food the giant hog lost versatility but its mouth could adapt more fully to grazing and this involved both lips, rhinarium and tusks (see drawing). Giant hog tusks have beaten a phylogenetic retreat from the prominent position they occupied in *Mesochoerus*. They curl out at an even sharper angle than in the warthog and the functional reason for the changed orientation was probably similar for both these grazers in that interference from the tusks during feeding could be reduced. Unlike *Phacochoerus* the tusks curve backwards well below the level of the nose and this has been of even greater significance for the morphology of the skull.

In spite of its droopy snout and lack of any direct relationship, the warthog resembles *Mesochoerus* in having long canines rooted near the front of the skull with tips that rise well above the level of the nose and in a high sweep of the forehead. The explanation for this is that fighting techniques were probably similar although the foreheads of the much heavier *Mesochoerus* are likely to have been opposed with greater violence because the eye ridges and temporal crests are disproportionately massive.

The *temporalis* muscles require neither ridges nor a long leverage and it is only leverage exerted at the front end of the snout that requires a tall occipital crest. Remove the role of the tusks and the activity of rootling and a high occipital crest becomes superfluous because the barrel of the snout is no longer a lever. Refinement of the mouth's cropping function therefore ushered in a collapse of the high occipital vault in the *Hylochoerus* lineage.

To compensate for its shortening the occipital lever arm had to move forward and this movement buckled the casing of the forehead. Such phylogenetic displacements or warping are perhaps facilitated by the fact that suid skulls have an outer shell within which self-contained zones of activity have their own bone capsules and these are separated by empty spaces traversed by thin supporting walls. This allows components to be reorganized and the outward form appears to adjust readily to the sort of changes I have described. As in the examples given in Volume I, (pp. 142—47) movements sometimes appear to leave their mark not only in kinks and lumps but in crepe-like corrugations or "stretch marks" on the surface of the bone.

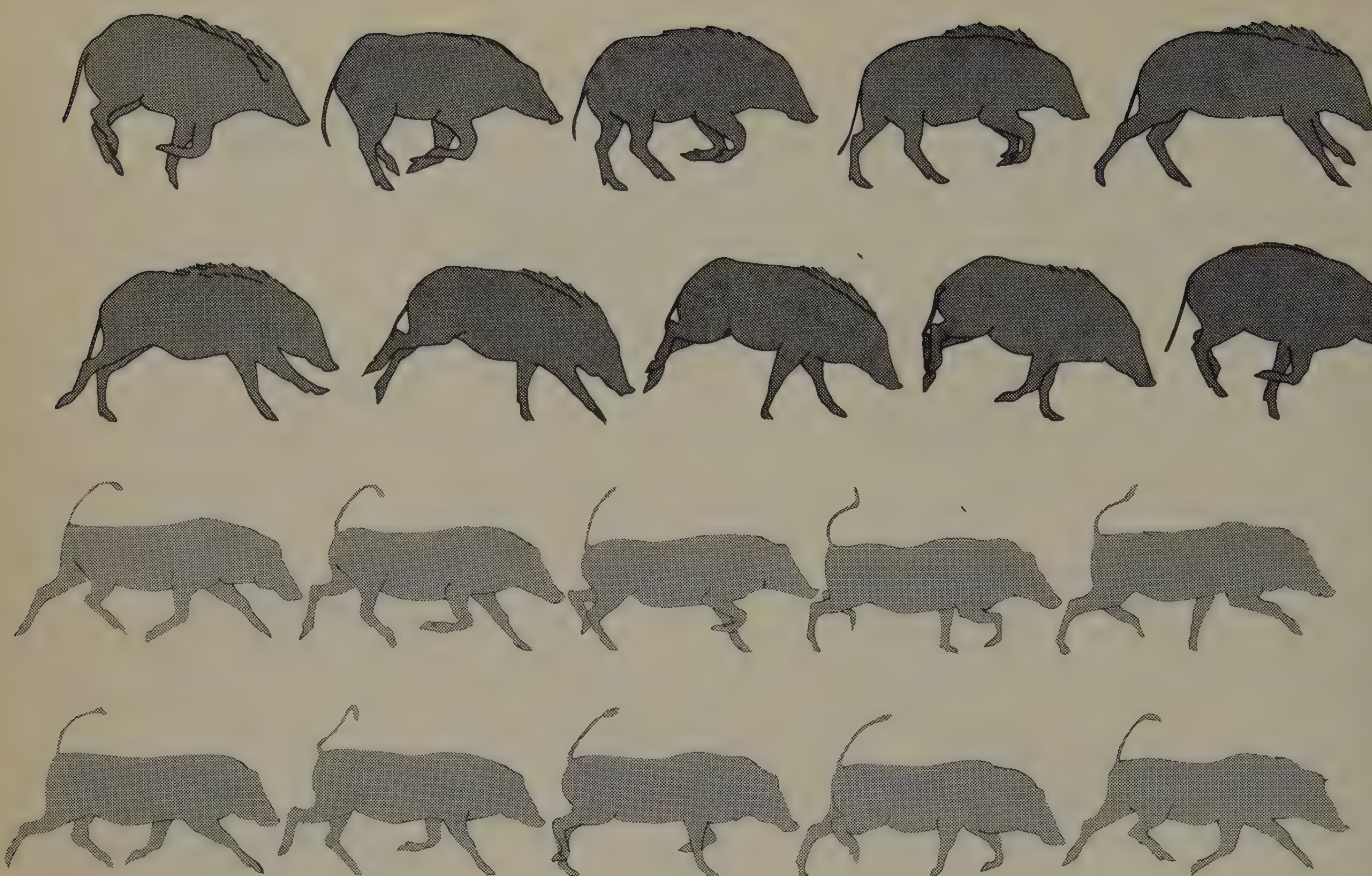


Cross-sections showing sinuses between the cranial capsule and the outer casing of the skull.
Above: *Potamochoerus*;
Centre: *Phacocoerus*;
Below: *Hylochoerus*.

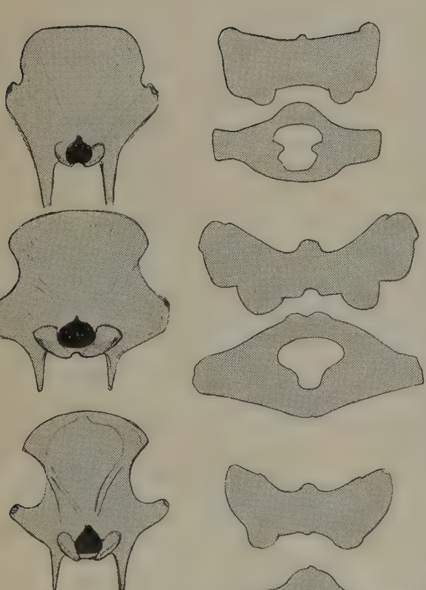
In this examination of the *Hylochoerus* skull in its evolutionary and functional context I have attempted to reconstruct the series of evolutionary changes that shaped the skull and to describe events in their approximate sequence. In this sequential chain the buckled forehead is almost certainly one of the last links. However, it would be misleading to restrict the explanation to a simple physical buckling in of the forehead under pressure from the migrating occiput. Had it been disadvantageous to be concave, the forehead could undoubtedly have bulged out or become flat but depression of the relatively thin forehead plate has also been a functional development and it is linked with the retention of massive mesochoerine temporal and brow ridges. These have been retained together with the cross-ridge of the occiput because forehead knocking, which was probably an important component in the tusk clashes of *Mesochoerus* has provided *Hylochoerus* with the means of testing the relative weight and strength of competing males. What is especially significant is that a mutual clash of vertical skulls has become a distinct ritual in *Hylochoerus*.

As in the warthog, the earliest stages of confrontation between males consist of a head-high approach with noisy tooth grinding or champing. Whereas an aggressive warthog raises its neck and depresses the nose the giant hog advances with its snout horizontally raised. These differences in the threat posture not only reflect different fighting techniques and skull dynamics but they carry the implication of a long evolutionary history which I have tried to reconstruct in a summary fashion in this profile.

Fully adult males quite often rush forward and clash their foreheads without preliminaries but a less abrupt sequence includes nostril sniffing followed by snout pushing and then snout knocking. Owing to the horizontal



Bushpig (upper) galloping and warthog (lower) running at precisely the same speed. Actions are exactly comparable as both animals were filmed in the same frame (film by Cumming).



carriage of their heads onslaughts are received and parried by the immense rhinarium. Like tusk wrestling in *Phacochoerus* or nose fencing in *Potamochoerus*, snout ramming in *Hylochoerus* is a ritualization of sparring but it has more restricted functions and is more clearly differentiated from the forehead clashing which only serves high intensity competition amongst males. Horizontal ramming is a more general test of relative strength and weight and adult males often break off an engagement at this point when one runs away. Other large ungulates as well as carnivores are frequently approached in the horizontal threat posture and sometimes rammed. The most frequent class of contestants, the young males, hardly ever proceed beyond snout knocking and attempting to knock their opponents head to the side. All of which reveals that every type of low intensity competition, both intra- and extra-specific can be settled by this relatively safe means.

The skull is well adapted for this activity. The barrel of the snout is reinforced throughout its length by a massive bony wall along its midline section. In older individuals this fuses at the front with an ossified rostral cartilage (which forms a mobile reinforcement for the sharp rhinarial disc in rootling pigs) thus providing a solid base for the vast cushion of the

rhinarium. The bullet-shaped profile of the skull and low occiput allow the impact of ramming to be absorbed straight back into the neck and vertebral column. This depends, however, on the pressure being horizontal and symmetrical. A slight downward deflection of the nose during a ram and it is possible for the forehead to jack-knife forward because the neck muscles have an insufficient purchase on the skull to withstand the force.

Such a mechanical interpretation is inadequate to explain forehead knocking which probably antedates *Hylochoerus*, having developed in *Mesochoerus* out of the sort of see-saw engagement that can be observed in *Phacochoerus*. A direct progression from snout knocking to forehead pushing normally only occurs in adult males but once head knocking has begun the climax of a headlong clash is soon reached. Boars rush at one another from as much as 20 m, retreating backwards after each impact and repeating the charge again and again until one gives way (see p. 211 for more detail). When the cupped foreheads are exactly opposed there is a loud report which can be heard over a long distance. Locals in hog habitats claim to hear this noise with some frequency which attests to the high degree of ritualization that has been achieved. Thick protective tissue on the cheeks, heavy ridges round the forehead, the median wall of the snout and a ridge down the occiput are clearly very necessary reinforcements against injury. Even so, skulls are frequently broken (illustrated are just two examples that are in my possession) and there must be particularly intense selection against males that are too fragile or too young to withstand forehead clashes. The restriction of clashes to fully mature males and only at the highest intensities of competition explains why two components of formerly continuous activity have become two distinct and very largely separate rituals.

Giant forest hog males with naturally healed broken skulls. Margin upper: left tusk and sheath fractured and displaced. Lower: right occipital casing broken.

Opposite page: back of the skull with outlines of the atlas vertebrae in (a) *Phacochoerus* (b) *Hylochoerus* and (c) *Potamochoerus*. Note the enlarged occipital condyles, the condensed body of the atlas and its flaring border in *Hylochoerus*, all adaptations that are well suited to absorbing the impact of forehead-to-forehead clashes.

Bushpig, River hog (Potamochoerus porcus)

Family Suidae
Order Artiodactyla
Local names

Nguruwe (Kiswahili), Inguluwe (Kinyiha), Inguluwa (Kirabai), Nguye (Kuamba), Nguve (Kipare), Ngubi (Kihehe), Ngorobe (Lukonjo), Mboye (Kiliangulu), Mbidzi (Luganda), Imbichi (Luhya), Epege (Ateso), Opegu (Madi), Opego-lum (Lwo), Tora (Kalenjin), Toroyet (Elkoni).

Measurements
head and body
127 (100—150) cm
height
55—80 cm
tail
30—40 cm
weight
70 (54—115) kg (males heavier than females)

Bushpig, River hog (Potamochoerus porcus)

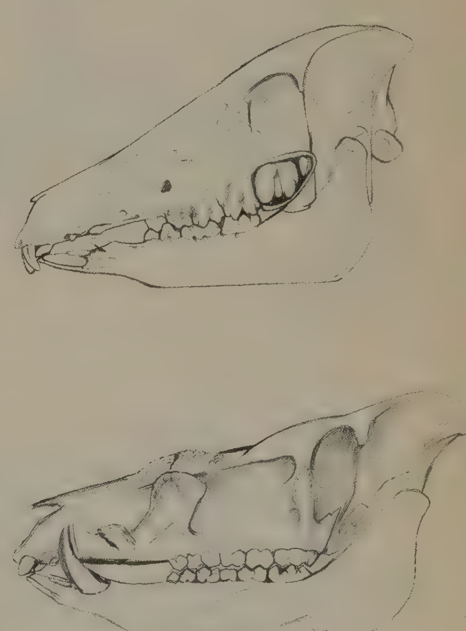
Races

Potamochoerus porcus porcus	Equatorial forests. Red. Patterned face
Potamochoerus porcus larvatus	Eastern and southern savannas. Grey. White face

The bushpig is an astonishingly compact animal. The slab-like, short-legged body tapers into the head and snout with scarcely an indication of a neck and the entire body seems to be galvanized into a single muscular effort when the animal rootles, fights or runs. The bushpig is the most typical representative of its family in that it is a true rootler. The western "red river hog" is also the most decorative of pigs, being a rich russet on the body with bold markings on the head. A white mane conceals a glandular area running down the midline of the neck. There are also white "spectacles" round the eyes, white margins and terminal tufts on the ears and a frill of white side-whiskers along the margins of the jaws. These markings stand out boldly against the black and red ground colour, whereas pigs from southern and eastern Africa tend to have almost entirely white faces and dark bodies. The southern form, *Porcus larvatus*, has been regarded as a distinct species by several authorities.

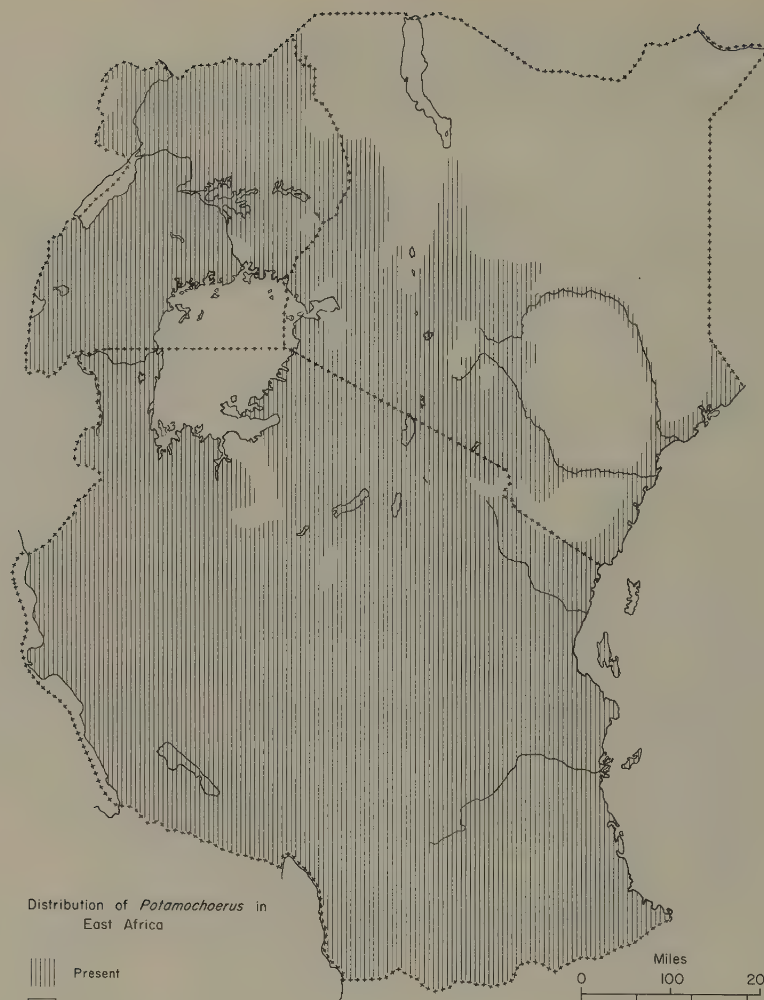
Over a large part of East Africa the bushpigs tend to show mixed features and the situation may resemble that of the bushbuck (map, next part) in that a dark grey, white-faced population with a longitudinal south-to-north distribution along the eastern half of the continent is overlaid by a red, face-patterned population with a west-to-east equatorial forest distribution resulting in extensive overlap and intermixing of the two stocks.

Dentition in juvenile and adult males.



Bushpigs live wherever there is sufficient moisture to support dense vegetation throughout the year and to keep the ground moderately soft. They are numerous in all forests, in most riverine habitats and in various montane habitats with thick cover. They live in reed-beds, marshes and mangrove swamps and venture into extensive papyrus beds, which may get detached and become floating islands. It is possible that Madagascar and Mayotte Island in the Comoros might have been colonized in this way. Bushpigs are also capable swimmers and could have reached Zanzibar, Mafia and the Lake Victoria islands in this way. It is interesting that they have failed to reach Pemba Island, which might have been protected by its deep channel and disadvantageous currents (see Moreau and Packenham, 1941).

Its ability to plough up soils and turn over heavy logs and other obstructions is made possible by the long but stoutly reinforced wedge of a skull, backed up by a very short neck and massive shoulders. The rhinarium is a sharp-edged and highly mobile disc and the end of the nose can dig, ram and explore by touch and smell. The latter senses probably determine what is taken into the mouth, which is wide and set back behind the tip of the nose.



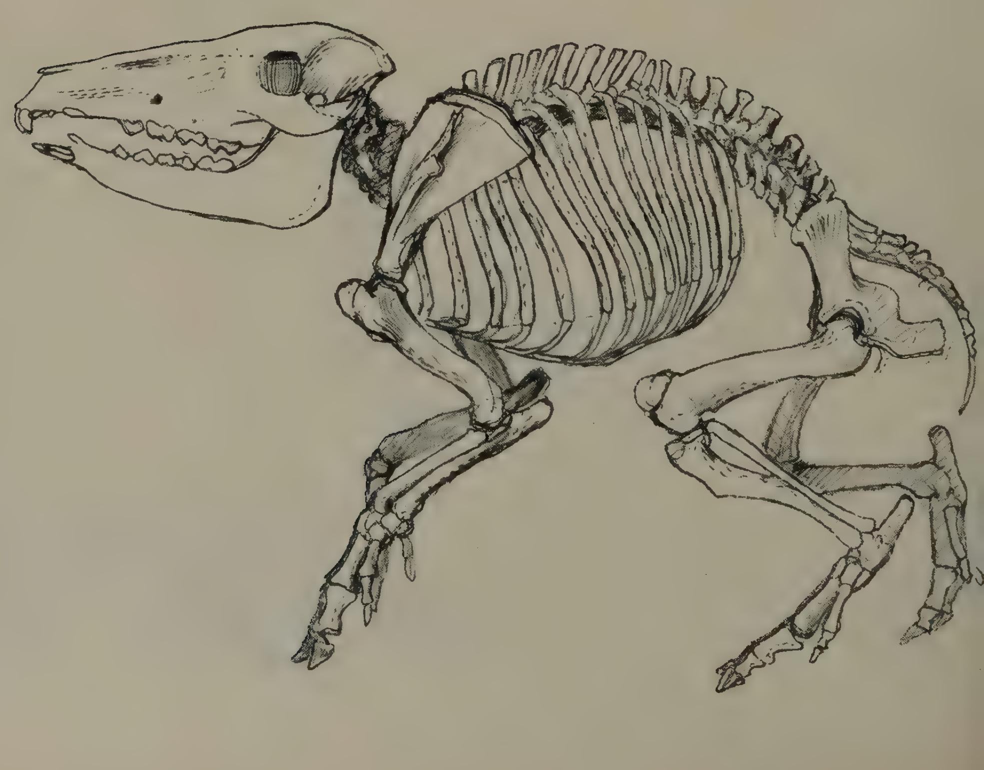
Distribution of *Potamochoerus* in East Africa

Present

Absent

There is continuous sniffing while the animals search and dig for food and visual cues are largely ignored.

Roots are the principal food of the bushpig; in central Tanzania, *Commiphora* spp., *Combretum*, *Lannea*, and *Vigna triloba* have been recorded (Harrison, 1936); aloe roots and *Chrysophyllum*, *Erythrina* and *Ficus* have also been noted. In Zululand, the tuberous roots of *Rhoicissus cuneifolius* are favoured. They also eat fallen fruit of almost any type and eat fern rhizomes and grasses that have a growth form that allows them to be pulled up and eaten in bulk. Thus some species are chewed up in entire tufts, while stoloniferous species, such as *Echinochloa pyramidalis* and *Ludwigia stolonifera*, have been seen being pulled out of flood waters by bushpigs that were up to their bellies in water. *Cyperus fastigiatus* is also taken (Scotcher, 1973). Of cultivated plants, groundnuts, maize, peas, beans and root crops are especially favoured. Papaya trees are undermined and felled for their roots, and, in parts of Uganda, bushpigs probably do more damage to cultivation than any other wild mammal. In addition to vegetation and fungi they will take a variety of animal foods. They rootle elephant dung for beetles as well as



recycling portions of it; they eat beetle larvae, giant snails and various amphibia and reptiles as well as eggs and bird nestlings, including ostrich, and small mammals. Carrion and bones are eaten and I have seen a pig holding carrion down with one foreleg while it champed and shredded the meat.

There is a record of a group of bushpigs chasing a leopard off its kill and they are known to have killed and eaten sick sheep, tethered goats and antelopes in snares. In this context it is very interesting that a captive group kept by Sowls and Phelps (1966) should have persecuted any injured animal, particularly if it had an open wound. Cumming (pers. comm.) saw a captive sniff the ground and then rootle out an old bone buried some 20 cm below.

Skinner *et al.* (1976) have noted the bushpig's ability to scent carrion over several kilometres and they reported *Potamochoerus* entering pig-sties in Northern Transvaal where they killed and ate domestic piglets. In this area they favoured the roots of grasses, *Hyparrhenia*, *Setaria* and *Fuirena hirsuta*, tubers of *Dioscorea* and *Drimiopsis* and the corms of *Cyperus esculentus*. They eat the fruit of *Sclerocarya*, *Landolphia*, *Antidesma*, *Ziziphus*, *Manilkara*, *Parinari curatellifolia*, *Garcinia livingstonei* and *Strychnos*, the last three having seeds distributed and propagated in the pig's dung. The pigs rootle much less while fruit is available but may dig deeply after juices have penetrated the soil (Breytenbach and Skinner, in press). Poultry and wild birds are sometimes killed but this is rare.

For those who have watched birds flocking after a plough, the following account suggests an interesting natural precursor of this activity. Harrison (1936) watched a large boar at Shinyanga "rooting up earth at a remarkable pace, in search of food, while around its snout was a flock of guineafowls picking amongst the loose earth as it was being thrown up, the boar being quite unconcerned and allowing them within a few inches of its snout."

The scarcity of observations on bushpigs is due to an overgrown habitat and to their being primarily nocturnal. In spite of this they may be active during the morning and evening in forest and other shady, undisturbed habitats and during the cool wet season. Adults spend almost all their active

Ear and face signals in bushpig (forest type). Above: ears horizontal and head up; below: ears vertical and head down.

time feeding or searching for food. When a single hog is disturbed, it generally grunts in alarm and rushes off, but in thick cover the pig may come to a halt after 20 or 30 m and turn round. Standing still, with ears spread wide it peers back towards the source of disturbance, sniffing occasionally and may then return, halting every few steps.

When viewed head-on, the white, triangular outline of the face is very striking and this visual emphasis on the head may help in the recognition of conspecifics and in the guidance of participants in head duels. The reinforced upper surface of the nose not only takes the strain of digging or turning up earth and litter, it also allows two antagonistic bushpigs to cross snouts and get a firm purchase on the flattened bridges of their noses. This apposition of snouts is assisted in the males by large gristly pads that cover the maxillary flange. These widen the area of purchase and may also protect the eye and maxilla when the opponent delivers blows with the snout. Actual contact is rare because one or other male tends to lose confidence in the ritualized display that precedes a clash. The boars tend to approach one another cautiously with crests raised and bodies bristling. Jaws champ and they paw the ground vigorously between short runs in which the tail lashes continuously, there are circlings and a series of advances and retreats interspersed with sudden breaks to lie on the ground and roll over and over (this presumably scents the soil). The boar kicks up the dust, slashes and tears at vegetation with the tusks and then leaps up to shake the body furiously with bristling fur and ears akimbo (Skinner *et al.*, 1976).

Fights are accompanied by a loud squeal, which is low pitched and can change to something like a roar. The noise may help intimidate rivals and is also heard from pigs caught in nets or pits (where it has been known to have a similar effect on hunters). The commonest sounds are typically porcine contact grunts; yet when not foraging they can be very silent and move away after an alarm with astonishing speed and stealth. A hand-reared captive kept by Cumming (pers. comm.) panted and made a very wheezy grunt as a greeting. This open-mouthed panting could be elicited by a human blowing upon its nose.

Contact grunts are uttered by the dominant individual within a sounder, irrespective of sex. In thick vegetation the grunts are made every five to ten seconds. Breytenbach and Skinner (in press) could discriminate between a threat grunt directed at squabbling young and a soft warning grunt that brought piglets running to the mother's side. A loud drawn-out alarm grunt precipitates flight.

The compact form and short neck of this pig not only affect its gait but also influence its mode of swimming, as the nose is normally carried well below the line of the back. The pig, therefore, swims with its head submerged and only raises it every 15 seconds or so to take a breath before continuing to paddle. Two animals swimming in the Nile were described by Pitman (1951) as swimming nose to tail with tails sticking vertically out of the water. Intercepted by a boat, they dived and swam underneath it, appeared on the far side and rapidly swam for the far bank, where they ran off through the papyrus. They did not seem to be affected by a strong current.

Wherever bushpigs live in extensive areas of forest, marsh or swamp, plant growth may be sufficiently thick and continuous to sustain a dense

population and allow small ranges. Such areas are often used continuously by the pigs and fields adjoining forests are often raided nightly while the crops are growing. On the other hand, gardens further afield may be visited but once and there is evidence that pigs living in narrow riverine habitats range over a considerable area. In the Transvaal Skinner *et al.* (1976) recorded cyclic use of a rootling ground, rotation taking place after about two months' use. Home ranges of 0·2 to 10 sq. km were estimated.

In addition to food, shelter, temperature and soil conditions being more favourable in the wet season (whereas all these factors are more restrictive in the dry), there may be seasonal changes in social structure that influence range and individual movements. Females seem to segregate themselves for the birth and early development of the young, but they may join up with other females in very large sounders before the young are fully grown. I have seen such a group numbering over twenty, which contained several adult animals and many half- or three-quarter-grown young. At least one large adult male was in this group and Dorst and Dandelot (1970) speak of a "master boar" and of sounders numbering up to forty animals. Solitary pigs are commonly seen as well as pairs and both mother-families and bachelor male groups have been reported.

In a study of the ecology of bushpigs on the shores of a Natal lake Breytenbach and Skinner (in press) recorded a mean sounder size of 2·6. They observed one case where a sounder known to be resident in the area was seen feeding on the carcass of a reedbuck while two other sounders were waiting their turn nearby. On another occasion a composite sounder of fifteen animals comprising two sows with two litters was seen. Skinner *et al.* (1976) suggested that sounders may be relatively stable with a regular annual mating cycle. During interactions between well-known sounders females and young accompanied their established boar and changes of alliance were not noted. Sows were seen to chase off strange sows and even challenge a strange boar. The dominant boar asserted his rights over his rootling ground and drove off all newcomers, "ownership of the feeding ground lasted only as long as the dominant boar was powerful enough to drive off other sounder leaders" and they recorded local dominance hierarchies between sounders. Within family groups the female and young tended to ignore one another but small juvenile pigs often associated with the boar.

Sanderson (1940) suggested that groups of pigs formed "teams" and moved heavy logs in concert. In fact, all feeding is highly competitive; while two or more pigs might strive to reach food concealed beneath a single log and might succeed in moving it further than by their own unaided effort, it seems more likely this is the result of competition than evidence of co-operation.

The facial area is well supplied with secretions, with one along the nape, another dribbling from the forward corner of the eye and a third coming from behind the maxillary flange. The pigs may transfer these secretions to one another in the process of mutual rubbing, nibbling of the mane or nose sparring, which is common between young pigs and partners of the same or opposite sex. Trunks, branches and rubbing posts may become scented deliberately through repeated scraping or involuntarily by the passage of the body. There are also carpal glands, which presumably scent the pathways

that connect feeding and refuge areas. Trees that are tusked by bushpigs average 24 cm in diameter and tusking is spaced out along short sections, some 10—30 metres of a pathway (Skinner *et al.*, 1976). Rubbing trees have larger boles. Bushpigs use latrines and walk deliberately to an established dung pile to defaecate.

The pocket behind the maxillary flange not only oozes secretion but also collects detritus from digging, and this has been said to provide a medium for the breeding of certain fly larvae in South Africa. Phelps also found nematodes in this pocket (Cumming, pers. comm.). In spite of their largely nocturnal habits, bushpigs are a favourite host for tse-tse flies and the animals have been observed to relinquish an exposed pasture to take refuge from biting flies. Bushpig blood has been found in the stomachs of tse-tses in several areas of central and eastern Africa. Bushpigs have presented a problem to game-extermination teams trying to eliminate tse-tse, as they are elusive, wary and difficult to shoot, poison or trap and are perhaps most effectively controlled by drives with nets and numerous dogs to rout them out of their thicket refuges. Cornered pigs raise their manes and roar and squeal with the nose lowered to the ground between their forelegs. Single dogs may be ignored by an adult bushpig and one observer saw a pig interrupt its feeding only to charge and butt a barking dog, after which it continued eating, having silenced the dog. In Toro, a party of wild pigs was seen to drive a leopard off a goat it had killed, appropriating the remains for themselves.

Rinderpest probably affected this species no less than the other pigs and populations may have fluctuated around the turn of the century. In Uganda, they were thought to be "peculiarly susceptible" to this disease (U.G.R., 1929). African swine fever is endemic in this as well as in other African pigs.

Leopards and pythons are the most important predators of adults, while smaller cats and eagles probably take many young. Lions and hyaenas are known to take them and might have a significant effect in controlling numbers in some localities.

Very little is known about their reproductive behaviour. Ansell (1964) published a gestation period of four months but this remains to be confirmed. Frädrich (1965) saw brow-to-brow pushing between a boar and a sow which he thought was a preliminary to courtship. Oestrous females present to the male and copulation is prolonged. In Tanzania and south-central Africa births have been reported between October and the end of January.

The female builds a nest or bower in which she gives birth. She makes forays from the chosen site (usually deep in a thicket or even in a hollow tree or rock crevice) to collect grass or reeds, branches or shrubbery. These she carries in her mouth and deposits in a heap, apparently compacting the stack of vegetation with muzzle and feet. After burrowing into this she excavates the centre, making a shallow dish in the litter and it is here that the young are born. Harrison (1936) gives ten as the maximum number in a litter. The piglets are very small and prettily marked with white or yellow spots on a black and brown background. The young remain in the nest for some weeks but growth is rapid. The spots have disappeared before they are six months old and adult weight ranges are reached in one year, although growth continues at a slower rate over the next year at least. In captives, sexual maturity can be reached at 86 weeks, the age at which one

female was estimated to have conceived (Sowls and Phelps, 1966). These authors published growth curves and tooth eruption sequences for some fifteen animals raised in captivity.

While they are spotted the young will crouch and freeze when the mother gives an alarm grunt and they stay crouched until the mother returns. This response wanes as they get older but fleeing hogs of near adult size have been reported to enter thickets and then crouch down until the last moment before fleeing again.

In spite of being a very important and abundant ravager of crops this species remains one of the least known of the larger African mammals. Its potential as a domestic animal should not be ignored and in my view it should have a high priority for further research.

Giant hog (Hylochoerus meinertzhageni)

Family Suidae
Order Artiodactyla
Local names
Nguruwe nyeusi (Kiswahili), Isengi (Lukonjo), Senge (Runyoro), Enshenge (Runyankole & Rukiga), Nsenge (Kuamba, Rutoro), Tumda, Tumwok (Sebei), Tumtu (Nandi), Tum (Kidorobo), Dumda (Kipsigi), Ol guya (Masai), Mbirri (Kitiriki), Numira (Kikuyu), Owil (Kakwa).

Measurements
head and body
180 (160—210) cm males
155 (130—200) cm females
height
96 (86—101) cm
tail
30—45 cm
weight
230 (145—275) kg males
180 (130—204) kg females

Giant hog (Hylochoerus meinertzhageni)

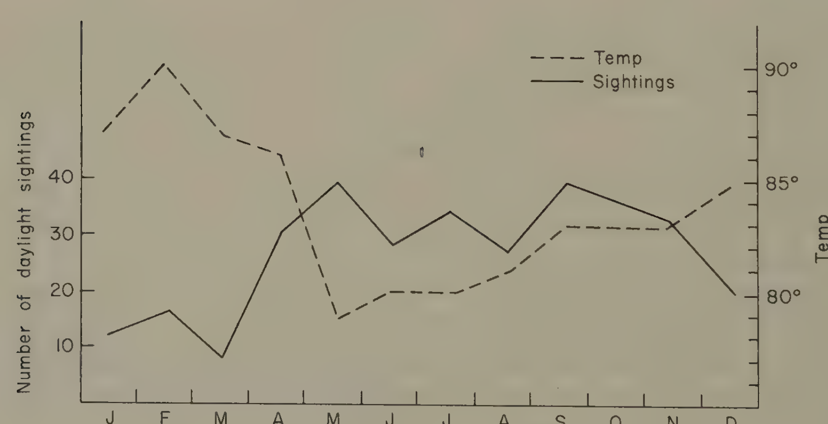
The largest living pig species, the giant hog is heavily built and covered in long black hair. Mature males are considerably larger than females and have enormous naked cheeks, a broad flat muzzle and tusks which emerge from the mouth horizontally and curve backwards in the same plane as the face. The snout ends in a swollen rhinarium that may be over 15 cm across. The female has a hairier and more slender face with much smaller tusks.

To an even greater degree than other species of pigs, the enormous difference between sexes can be correlated with intense and continuous competition amongst males. The peculiar manner in which the boars clash their heads together allows a functional explanation for the flat plate-like surface of the male's head and its great breadth. When boars meet in the presence of families of females and young, one or other withdraws or they put their foreheads together and push until one gives ground and flees or else they back off and charge one another from a distance. The impact usually rocks one or other of the rivals back on to his haunches. If the heads meet in exact opposition there is a loud report and this noise is made by compression of air within the dish-like hollows on the forehead that are highly characteristic of giant hogs (the evolution of which has been discussed earlier, p. 185). If the first charge is not decisive, both boars back off about 30 m and, ears back, manes bristling out all over, they then charge again. These contests have been seen to last up to half an hour and in one fight watched by Maloba (pers. comm.) he noticed that the stronger animal spurted urine with each clash. Like other male pigs in a state of excitement, they champ their jaws and spittle flies as the heads thump together.

Prominent on the flat face of a mature male are grotesquely swollen pre-orbital glands, the secretions of which are stimulated or perhaps forcibly expressed by the blows of the head clashes, for they are certainly not shielded in any way. Their primary function seems to be to advertise the male's condition and when a victorious male rejoins the sounder his pre-orbital glands, his saliva and perhaps genital scents are smelled by the submissive females, meanwhile subadult males avoid him.

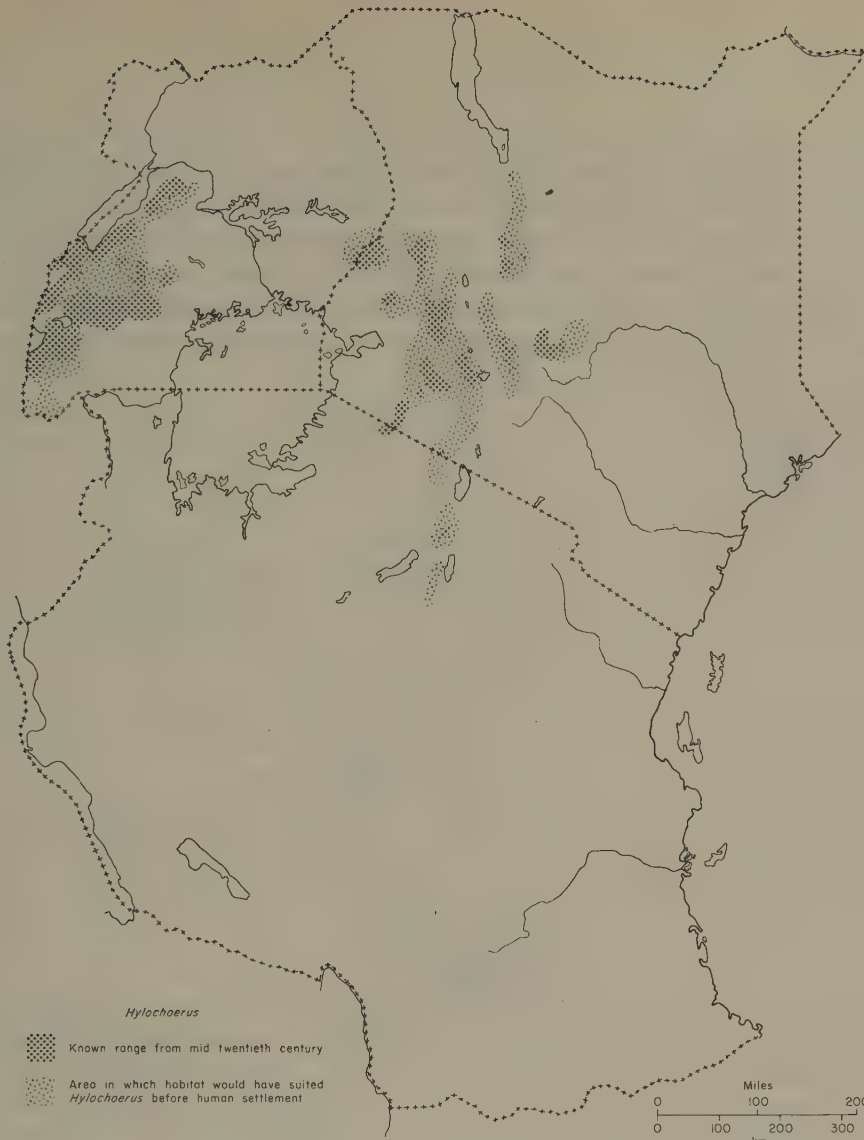
The social structure and behaviour of this animal is adapted to a life that alternates feeding on lush vegetation in relatively exposed habitats with sheltering in dense undergrowth or scrub; it is by no means exclusively a forest animal.

The giant hog is scattered across tropical Africa in a series of rather localized populations inhabiting various vegetation types, from subalpine areas and bamboo groves, through montane to lowland and swamp forests, galleries and forest savanna mosaics, wooded savannas and post-cultivation thickets. The ecological separation of the three species of pigs in Bunyoro has been discussed in the suid profile. A yearlong and plentiful supply of green fodder and dense cover are found in all localities where giant hogs occur. They are sometimes quite numerous and in parts of the Aberdares are one of the dominant herbivores. They live in cold uplands as well as hot lowlands but they do not tolerate low humidity or prolonged radiation. They are not nocturnal but there is evidence of seasonal change in their activity cycles. Some measure of their avoidance of direct exposure to the heat of the sun has emerged from records kept at the Ark, a viewing lodge built above the Yathabara glade in the Aberdares. I am indebted to the director and staff, the Park Warden and rangers for access to the lodge, Park and information. Most particularly R. J. Prickett has generously provided me with detailed records and many interesting observations. The diagram below correlates

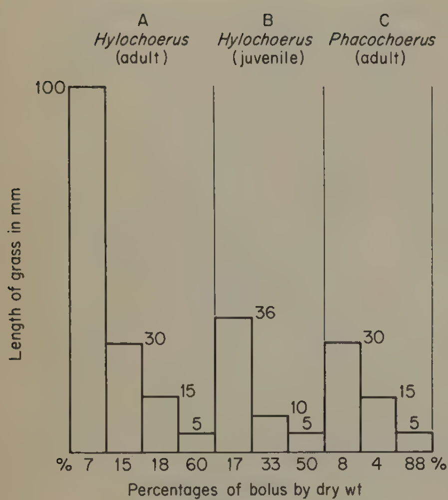


Hylochoerus visiting Yathabara glade. Record of number of groups sighted by day in 1974 correlated with average maximum temperatures for the region.

daylight sightings with temperature. At the end of the dry season in 1974 only 5% of the Yathabara sightings were recorded during the day. At other times of the year hogs grazed in the afternoons and evenings and as many as



27% of the sightings in September 1974 were during daylight. Peak activity is from dusk to nearly midnight and feeding animals have been seen to graze for up to four hours (Prickett, pers. comm.). It is possible that one old boar, which regularly grazed at Yathabara might have satisfied his feeding requirement in that time. Occasionally, when there have been prolonged periods of mist, rain or cold, hogs have been seen emerging into the open simply to sunbathe but there are generally fewer animals active during the mornings than at any other time and Stockley (1952) described finding sounders piled up for warmth under clumps of bushes on cold mornings. They do not emerge from the bush on very cold, wet or misty nights unless there is a succession of such nights. Yathabara glade has a natural pond and abundant grazing and it is surrounded by dense evergreen thicket dominated by *Crotalaria*, *Solanum*, *Vernonia* and *Cassia didymobotrya*. This secondary growth covers about 70% of the surrounding country with patches or galleries of montane forest. About 20% of the land is grassed and this pasture is maintained by buffalo, hogs and other grazers. They prefer to graze off mats of relatively short grass but they are able to feed on many species of grasses, sedges, and herbs and are able to crop them at various stages of growth.



Differences in grass selection and mastication in (A) adult *Hylochoerus*; (B) juvenile *Hylochoerus*; (C) adult *Phacochoerus*. In (A) coarse leaf and stem abundant, fair mastication; (B) young green leaf selected, poor mastication; (C) fine mastication of leaf and stem.

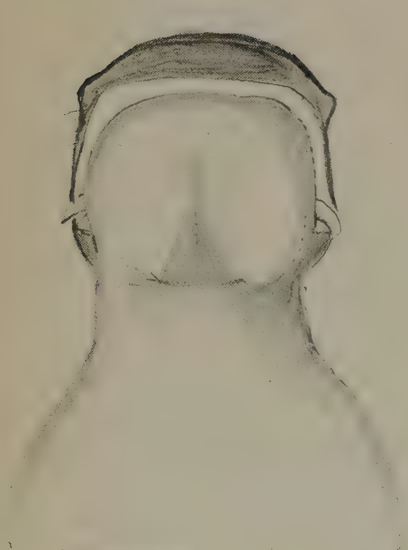
I have observed hogs grazing on short grass in the Ishasha area of the Ruwenzori National Park and the dominant grasses that are subject to heavy grazing in this park have been identified and annotated by Lock (1970). These species are also dominant in the forest–grassland mosaic in Bunyoro and the list below probably includes most of the major grasses eaten by *Hylochoerus* in Uganda. (No study has yet been made of which species may be preferred or selected and the list may include species which are not favoured by giant hogs.)

Aristida ascensionis	annual
Brachiaria spp.	heavily grazed
Chloris gayana	heavily grazed
Commelinidium mayumbense	forest grass in deep shade
Cynodon dactylon	heavily grazed
Eragrostis tenuifolia	common in overgrazed areas
Heteropogon contortus	tall spp. but new growth grazed
Hyparrhenia spp.	tall spp. but new growth grazed, very abundant
Imperata cylindrica	only new growth palatable
Microchloa kunthii	common under *Themeda*
Panicum maximum	heavily grazed in pans
Paspalum conjugatum	short forest grass heavily grazed
Setaria sphacelata	shade-loving species on margins of forest
Sporobolus pyramidalis	the dominant valley grass
Themeda triandra	fire climax spp., only new growth heavily grazed

In montane areas with abundant herbaceous growth grasses might play a smaller part in the diet of *Hylochoerus*. On both Mt Kahuzi and the Mau the herb *Mimulopsis* (Acanthaceae) has been reported as an important food (Rahm and Christiaensen, 1963; Simon, 1962). Lianes, bamboo shoots and members of the Cyperaceae and Melastomaceae have also been recorded. However, in the Aberdares I found grass only in over 100 dung samples.

In these samples I found that adult hogs ingest more grass stems and mature grass leaf, whereas a single juvenile sample showed a high proportion of younger green grass leaf with very little stem and the grass very poorly masticated. Warthog dung from the same pasture was also composed entirely of grass, mainly leaf, but the material was much more finely masticated in this species, which has higher-crowned molars that are better adapted to grind grass.

Lower jaw



The normal cropping action is a short downward nod of the head. The grass is seized by the lips and is broken against the hard sharp margin of the upper lip. When they feed on long green grass, they sometimes raise and twist the head slightly to tear a mouthful away and then champ away at it with the usual nods. Rootling is rare and when the snout is used, it is in soft mud or humus or to excavate salty earth. However the main agents in the excavation of earth are the flat, forward-pointing lower incisors. I have examined shallow caves, entirely excavated by forest hogs, in which the distinctive marks of their lower incisors as well as tusk marks could be recognized. The caves consisted of an overhung bank, sometimes in the embankment of a deserted road or river bank, sometimes in the earth-filled root system of an overturned

tree. The hogs' activity is most obvious in irregular recesses cut further into the bank between about 50 and 100 cm off the ground.

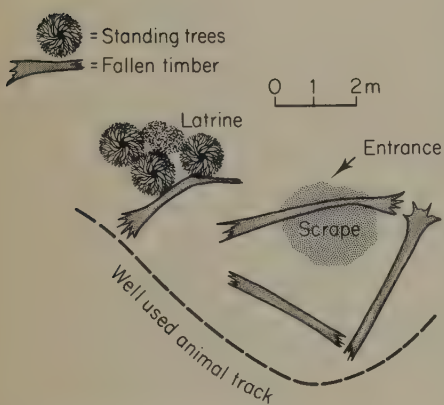
When salt was first put out to attract animals into Yathabara glade it was not immediately noticed by the hogs and a taste for the crystals was only acquired over many months. However, salt eventually appeared to become a major incentive for the hogs to visit the lodge area. Occasionally they nibble bones or eat meat and insect larvae; Prickett (1974) has watched a boar pulling at one end of a newly killed buffalo's ribcage while a hyaena tugged at the other and it was the hog that finally succeeded in gaining possession. Bones may be steadied with a foot while the meat is shredded off with the incisors.

Paths used by *Hylochoerus* and other animals to visit Yathabara glade. Texture indicates forest; black indicates grassy glades; rest indicates dense thickets.

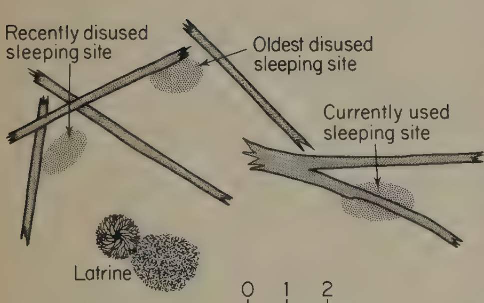
Of the *Hylochoerus* dung that I examined in the Aberdares about one in twenty contained earth and in several instances the bolus was only sparsely laced with grass.

Dung is seldom dropped at random; favoured dung-sites are generally at the base of a tree or under a thicket. The largest and most frequently used dung deposits are communal "latrines" within a few metres of the sleeping site. Along the margins of pasture there are also a number of deposits which are used by more than one animal. In the Aberdares I was shown two very

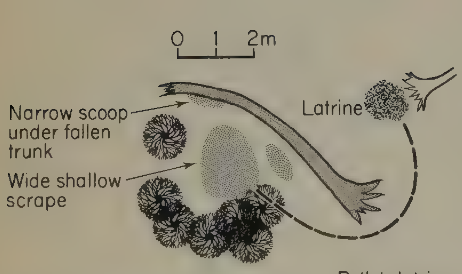
Diagrams of sleeping sites referred to in text.



Sleeping site near animal track



Longterm sleeping sites in tangle of fallen timber



Frequently used sleeping site in dense forest

well-established latrines at the base of large trees on the margins of a grassy watering place. An experienced local observer (Muhangia, pers. comm.) stated that they were used immediately after drinking.

The size and number of latrines near sleeping sites are variable and depend on the frequency with which the place is used and the number of animals using it. The action of weather, termites and dung beetles ensures that few deposits remain recognizable for more than a few weeks without being augmented.

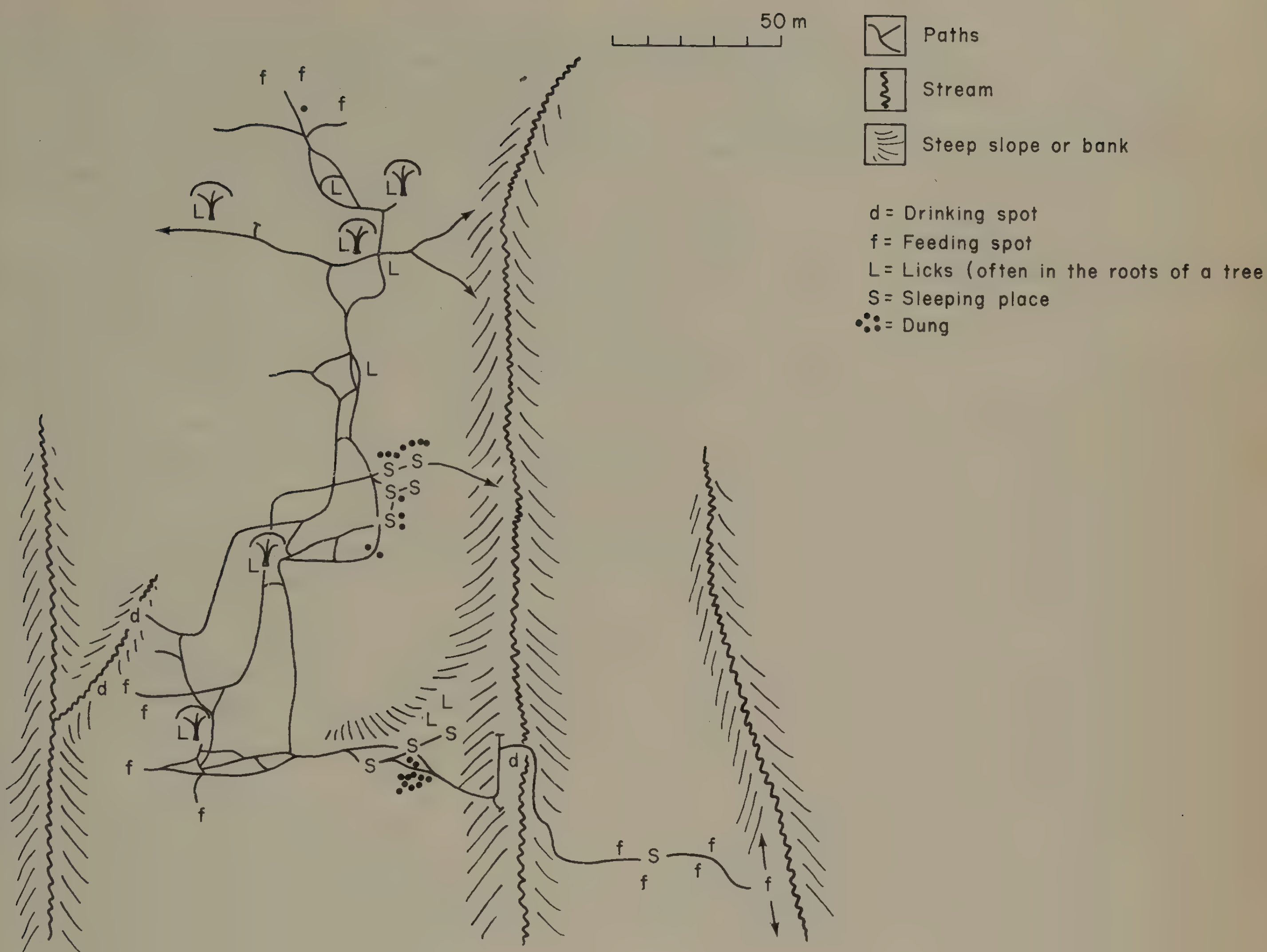
Deposits may serve to advertise the occupancy of a sleeping site but a more important social function may be served. Not only are the sites changed frequently but the sleeping partners also change because family groups associate with a variety of neighbouring families and can change these associations from day to day. Scent cues in the dung might acquaint individuals and perhaps even help forge temporary bonds in animals that sleep piled up together in very close bodily contact.

Preferred sleeping sites are under fallen tree trunks with a protective barrier of vegetation on at least one side. A shallow scoop of bare earth made with the rhinarium is common and this may be up to three metres across but is usually less than two metres and oval in shape (see diagram).

Sleeping sites are used during the middle of the day and may also be used for a few hours after midnight. In very cold wet weather the animals may remain inactive for long periods.

On the assumption that giant hogs were territorial, Mohr (1960) described them rubbing "boundary trees" but in fact all classes of pigs spend much time rubbing themselves and the choice of sites is more likely to be determined by the presence of stumps, banks and termitaries beside paths and other centres of activity. Rubbing is clearly rewarding to the pig itself but glandular secretions (from the face and anal region in particular) are readily transferred and a limited number of suitable posts and pathways probably ensures that all the animals within a locality become acquainted with one another's scent. Prickett (in lit.) has noted that piglets often present their posteriors to the mother's snout and rub against it, even while she is grazing—behaviour that suggests an element of submission.

The animals' sense of smell is acute and many social interactions are likely to be regulated by animals responding to one another's scent. Hearing is also very acute while vision is of subsidiary importance. Regularly used communal dormitories are scattered through the home range. Rahm and Christiaensen (1963) have mapped such a locality on the steep slopes of Mt Kahuzi, Zaire. A network of paths linked the sleeping areas and connected mineral licks and grazing grounds on the peripheries of the mapped areas which totalled some 7,500 sq m. Subsequent investigations have suggested that such a small area probably provided the core area for a single family but this does not preclude its use by others. Ionides (1965) thought that they wandered long distances but wound about in the forest while doing so. Kariuki (pers. comm.) has suggested a range of approximately 10 sq km and Dönhoff (1942) described hogs as strictly sedentary but with a large range. D'Huart (in Montfort, 1974) has reported seasonal movements after food.

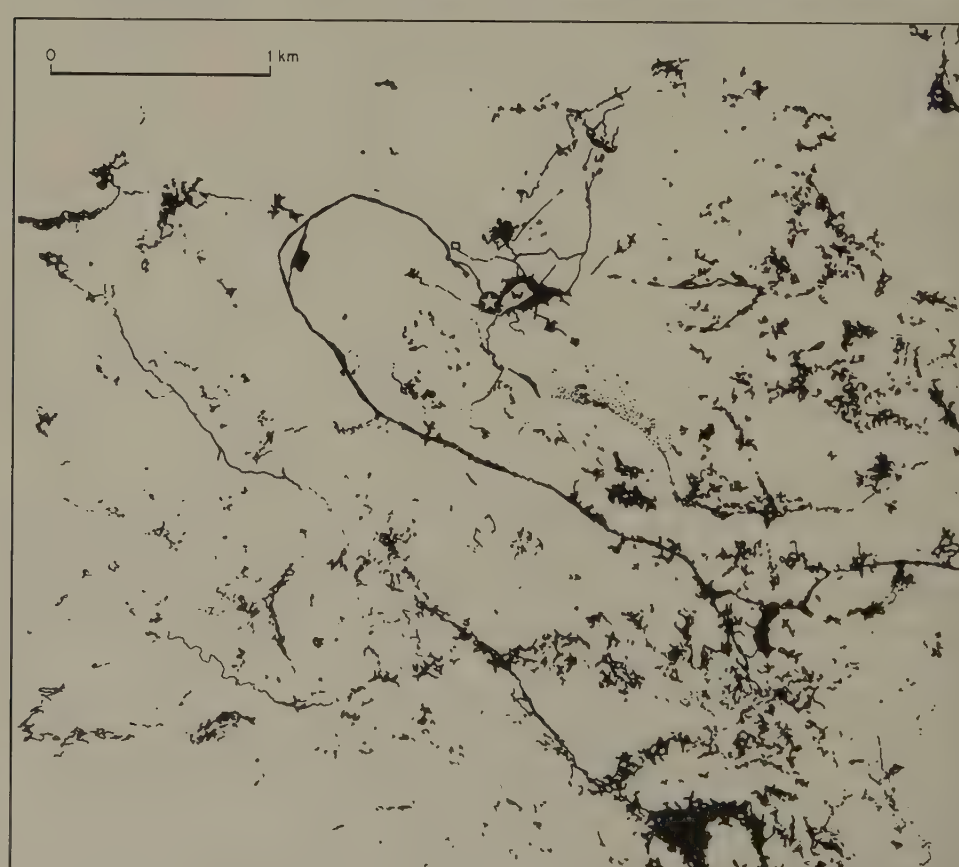


Paths and landmarks in *Hylochoerus* habitat on the slopes of Mt Kahuzi (after Rahm and Christiaensen, 1963).

The basic social unit is the mother and her offspring of up to three generations. At Yathabara 96% of the families are accompanied by a male and it is unusual for there to be more than one mature male in a sounder. In dense cover families tend to be dispersed singly but common grazing, water and mineral licks are likely to provide local foci for a number of single males and for families, all of which are constantly meeting one another.

Within any given area the males probably take one another's measure from an early age and past experiences may underlie ready retreats by one boar from another. Prickett has noticed that when two sounders meet, the boars become alert to each other at about 30 m whereupon one usually withdraws followed by the female and young. However families are not strongly attached to the boar and a condition of the environment that pro-

vides a strong attraction can cause families to amalgamate temporarily. Even in these enlarged assemblies there is generally only one boar, although several others may be nearby. Prolonged associations between more than four or five females are unusual. In the Yathabara glade as many as forty animals have been seen together at one time but this is an extremely rare and temporary event. From observations at the Ark in September 1975 and from subsequent records provided by R. J. Prickett I determined that about seventy animals visited the area near the lodge in the course of the month of October. The exact number of large boars was uncertain but might have been in the region of six to ten. There were thirteen families which could be recognized by the age and number of the young and at least three females without offspring. Since no family contained more than three generations of young nor more than eight members I was able to identify each one with a three-unit code according to the numbers in each generation. (The last unit was reserved for very young piglets, the first unit only for the oldest young in two or three generation families.) Only three of the families and a single female came with great regularity and a high proportion of the sounders included these four groups in various combinations. There was a neat graduation in the number of associations formed by each family and this suggests that the ranges of the numerous families comprise a series of overlapping foci, each family having a core area but ranging over a much larger region where it may link up with other families; in this respect giant hogs resemble warthogs. Artificial park boundaries define the northern and north-eastern limits of the Yathabara



Pastures in the vicinity of Yathabara glade. Giant hog densities are greatest south-east of the glade. Grassland (including roadside verges) indicated in black. * = the Ark viewing lodge.

population; the western, southern and south-eastern catchment area is less certain. The possibility of "clans" similar to those of the warthogs (Cumming, 1975) awaits investigation.

The diminishing order in numbers of associations is illustrated below and the families are listed by their code numbers. These can be correlated with the table of association frequencies below.

Family 013	23 associations
Single female A	19 associations
Family 004	17 associations
Family 020	17 associations
Families 010A 010B	8—11 associations
Family 220	9 associations
Single female B	7 associations
Family 060	5 associations
Family 050	4 associations
Single female C	3 associations
Family 002	3 associations
Families 030A 030B	1—3 associations
Family 041	2 associations
Family 340	1 association

Identifiable associations, including the same adult male have been recognized by resident observers. Over quite a long period Thairu (pers. comm.) noticed that one party of ten animals always came along a particular path and he thought that they might have been the tenants of a well established sleeping place in a patch of dense forest less than a kilometre to the north of the glade.

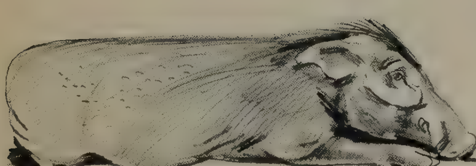
Short-term regularity in the number and sequence of groups visiting the glade can be illustrated by records from 12—25 May 1976.

DATE	DAY	NIGHT
May 12	2	12 9 6
13	2	1 12 5 1
14	2	9 6 7 5 1
15	—	1 12 2 5
16	—	13 9
17	1 3	1 4 10 7
18	1 2	13 9 1 7 9
19	1	10 2 4
20	4	8 1
21	6 1	9 6 2
22	3	9 6 2
23	3 1	9 1 4
24	—	8 9 7 3 1
25	7 3	9

Associations of more than about twelve animals are rare and generally signify the joining up of more than one family group. The group members seen on nights before or after visits by such enlarged sounders reveal the very temporary nature of these amalgamations.

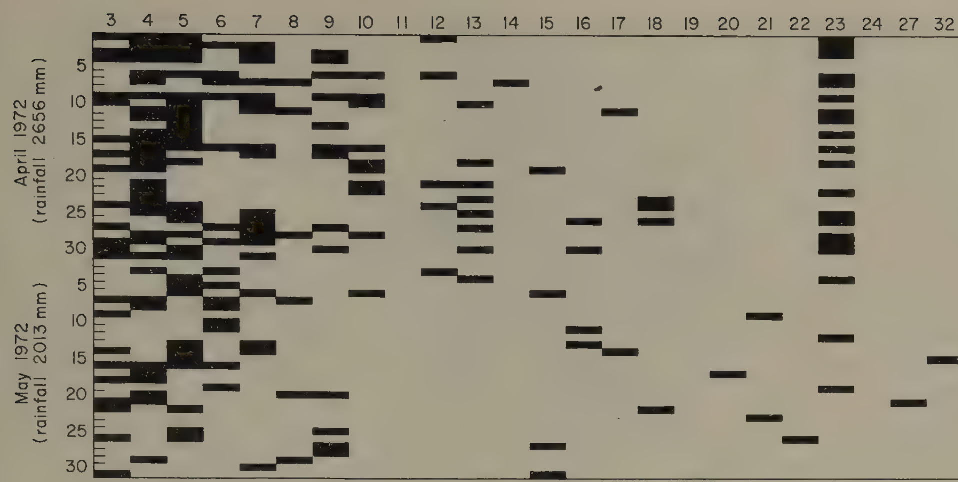
Date	Groupings	Total numbers of animals
March 6th 1974	15–1–1–2–6–3	28
March 7th	4–1–5–6–8–3–1	28
May 23rd 1974	21–3–2	26
May 24th	5–1–1–4–3–2–11	27
July 28th 1974	8–2–5–4–3–1	23
July 30th	18–3–1–5	27

There is also evidence that amalgamation of family units is a commonplace in the life of giant hogs. Considering all those nights in 1971 in which at least four sounders visited Yathabara, the first two sounders to emerge from their daytime retreat contained an average 6·4 pigs. By contrast the average numbers recorded in the last two sounders averaged 6·8 pigs. During more restricted periods there are still greater differences.



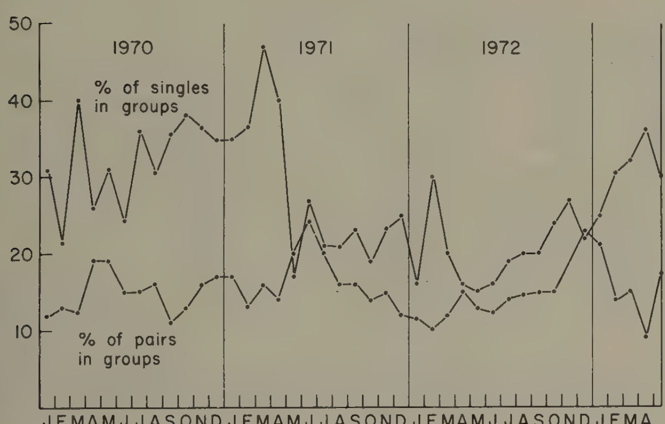
Because piglets are continually disappearing the families change their sizes. Individual social units are difficult to identify but one exceptionally large family in Yathabara has also provided information on how family units sharing a common home range form favourite associations, parting and joining up repeatedly in certain particular permutations.

In November 1971 a female with a litter of eleven small piglets first appeared in the Yathabara glade. This family moved in the company of between three and twenty other animals and the number sometimes changed in the course of one night but they most frequently ran in a sounder totalling twenty-three pigs. Prickett (in lit.) noted that the uniformly sized piglets consistently followed one sow and only sucked from her, so the piglets were presumably a single litter. Although females occasionally suckle the progeny of other sows, this family was never accompanied by animals that were less than half-grown. This family and its associates maintained their numbers for nearly eight months. The latter were not another single family but were instead a composite group. That these pigs did not maintain a group identity apart from the family was shown in the near absence of records for a sounder of eleven. The family was never joined by mating pairs, so that fourteen was a rarely recorded number and the rarity of nineteen, twenty and numbers in excess of twenty-three revealed that other families in the neighbourhood were limited in number. Frequent associations with groups of three to six corresponded to the existence of several family units numbering two to five (exclusive of males). All other recorded sounders were likely to be combinations of these or more distant families on transient visits. This pattern could probably be demonstrated for other years and other populations but the unusually large family made relationships clearer and the pattern of their association over two months is shown in a graphic form opposite.

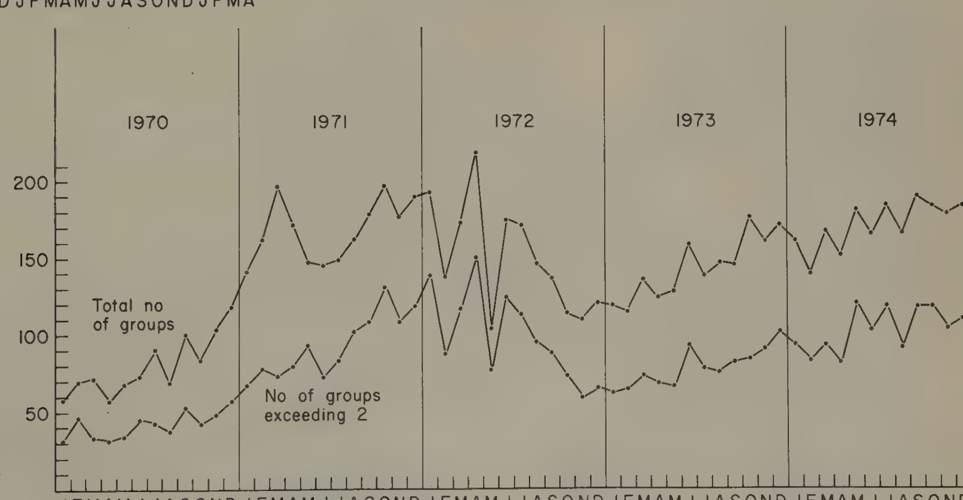


Group numbers visiting Yathabara glade in April and May 1972.

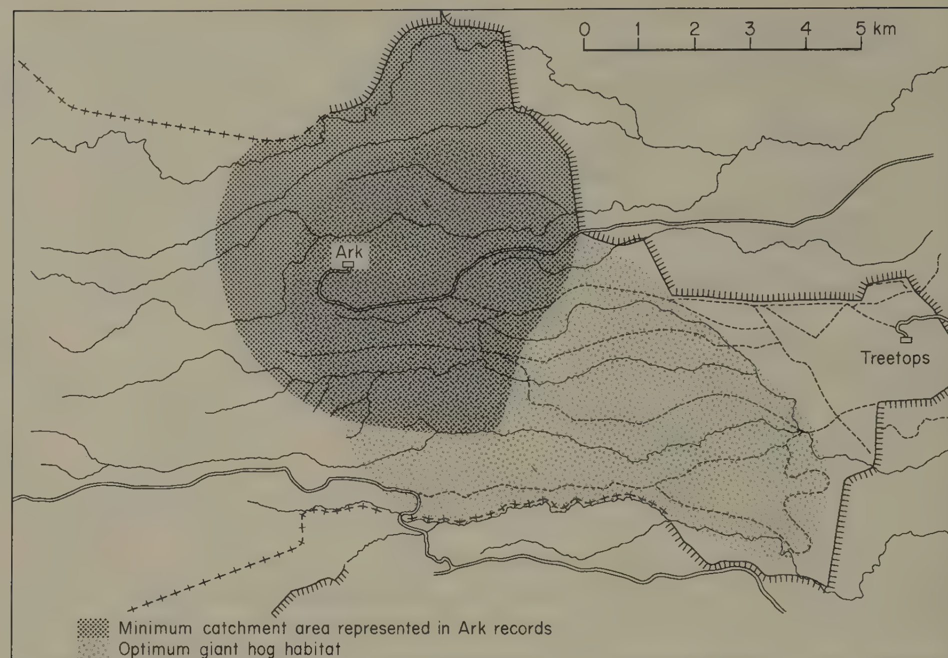
The records also provide some insight into population changes. In the two years following completion of the Ark in 1969 there was a progressive increase in the number of hogs visiting the glade. A single large sounder making nightly visits soon inflates the recorded number of animals into many hundreds so that total numbers are no guide to events. The number of groups is a more reliable indication but the cold months see a fall-off in activity (see April—May in diagram). Group numbers are disproportionately affected by a preponderance of single animals or pairs but this is itself significant.



Left: percentages of singles and pairs in groups, 1970—1973, Yathabara Glade.



Right: numbers of groups visiting Yathabara Glade.



An interesting pattern has emerged from comparing the records of total group numbers with those for groups in excess of two. Visits from the latter, which are family sounders increased at a very steady rate over two years from an average of little more than one family a night in early 1970 to four sounders a night by the end of 1971. Solitary animals, effectively the males, started using the glade in greater numbers earlier than this and the average was as high as three boars a night in March 1971, but there were several extreme fluctuations in the number of visitors. Cold weather was one influence but the build-up of numbers of boars may have generated its own forces which are reflected in the extraordinary oscillations of male numbers at that time, contrasts which have not been repeated again.

The glade attracted peak numbers of pigs for nearly a year but between June and November 1972 a sharp decline was recorded. After this the population recovered its numbers more slowly than before, since which a very much more even pattern has been apparent. After the disturbances of building and road-making the glade was probably recolonized by pigs from more than one area and the lack of equilibrium evident in the earlier phase could have been due to a lack of established relationships between the animals using the glade.

The general decline in 1972 might have been influenced by disease. Pigs have been found dead in the vicinity of the glade, untouched by the relatively abundant spotted hyaenas but they were assumed at the time to have died of old age.

The Wanderobo hunters in the Mau forest state that the plant *Mimulopsis* which has a mass flowering at irregular intervals up to seven years apart (see Volume I, pp. 26—27) kills large numbers of giant hogs and bongos in the second year after it dies back. They also claim that they themselves are affected by a severe hay-fever during the flowering and that old people and young children may die from the effects. Simon (1962) was able to confirm the effects of *Mimulopsis* (*Setyot*) on the giant hog and bongo:

> "This was the second year of the *setyot* cycle and there was evidence of scouring among the bongo and giant forest hog and several corpses of both animals were found. Samples of *setyot* were collected for laboratory analysis, resulting in a report that the plant material was definitely toxic and an extract of one gramme of the wet stem was sufficient to kill a mouse after first causing chronic diarrhoea."

As this is a dominant food plant for both mammals their mortality might be quite high.

Fluctuations in the size of the forest hog populations are known to have occurred but are poorly documented. In 1947 they were noted as very numerous in the Aberdares. Whereas they had formerly been limited to the upper forests, they began to be seen below the 1,800 m contour and started to raid cultivation. There were similar reports on their abundance in Uganda at this time but it is possible that the increase in population may have been checked by rinderpest outbreaks. There is evidence that populations may have been severely hit by some of the rinderpest epidemics that affected parts of eastern Africa in 1923, 1926, 1935, 1951, 1953 and 1960 and it is possible that the animals' patchy distribution might have been influenced by disease. Giant hogs are also susceptible to African swine fever and it has been suggested that, in common with other wild pigs and *Orycteropus*, they might form a reservoir for this disease. Giant hogs are parasitized by a species of *Trichinella*.

Ecological and dietary limitations are also likely to be important determinants of the hogs' distribution. Their co-existence with a wide range of other ungulates suggests that in a rich habitat direct competition is probably negligible. However, if shade, shelter and green fodder are dispersed or of poorer quality at any time then physiologically more advanced grazers may be at an advantage and in these circumstances competition may help define the ecological boundaries of the hogs' range. The buffalo is the commonest grazer in all parts of the giant hogs' range. I have already mentioned the role of this animal in maintaining "buffalo glades", which also provide grazing for the hogs. Giant hogs commonly interact with buffaloes and Prickett (1974) has seen a male butt one in the buttocks. As butting is intrinsically intra-specific behaviour and the two species commonly graze side by side, such incidents have more the character of play-like competition than aggression but there is also a more concerted action against large ungulates including buffalo, rhino and bongo which has the appearance of mobbing competitors.

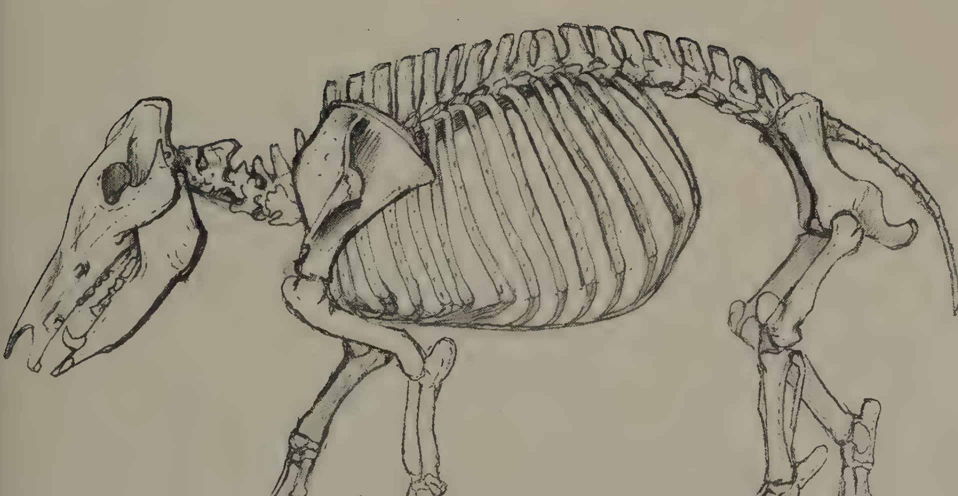
> "The whole sounder moves up slowly in a semi-circle with snouts held well out. They then halt at about thirty feet. One animal, usually a half-grown beast, moves up deliberately and sniffs under the victim's tail. In the case of buffalo and rhino they usually all flee towards the bushes the moment the beast turns round. This may happen also with bongo but often bongo bound away and, as soon as the hogs realize this, they give chase, boar first and the rest of the sounder trailing behind. However, bongo sometimes refuse to be intimidated and stand their ground with lowered head. Once a bongo bull was seen to charge a giant forest hog and strike him hard with his bony poll just below the horns. The hog squealed loudly and fled." (Prickett, in lit.)

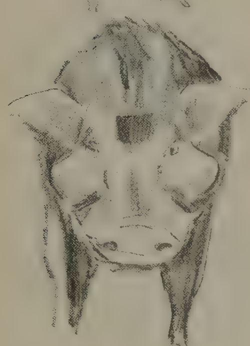
At the present time giant hogs are abundant on the Aberdares and are the dominant pig above 2,000 m. Below this warthogs are more numerous and the table below compares sightings at two viewing lodges above and below this line.

	Treetops 1,870 m	The Ark 2,300 m
Warthogs	1,873	213
Giant hogs	166	1,053

The records are for July 1972 but are probably broadly representative of the relative proportions of species. Bushpigs are very shy, normally do not graze and are strongly attracted to salt but, notwithstanding this, the sighting of only two animals at the higher lodge in four years is indicative of the relative rarity of this species which is, instead, conspicuous and numerous in comparable montane habitats where the giant hog is absent. In spite of having very different feeding regimes and co-existing in lowland habitats further west, it seems likely that giant hog concentrations depress bushpig populations in the Aberdares, a phenomenon that I believe may be due to competition for secure shelter (see p. 185).

The disappearance of a high proportion of piglets suggests that predation on the young is very considerable in spite of vigorous defence by the sows and particularly by the boar. At Yathabara sounders with small piglets are





seldom seen during periods of full moon and they run away at the slightest disturbance. They are particularly sensitive to the presence of spotted hyaenas and leopards. Attacks or mobbing of sounders by hyaenas have been observed in Yathabara glade on numerous occasions and Prickett has seen adult animals surround the youngsters when hyaenas advance. The boar often rushes out and chases for distances of up to a hundred metres before returning. The increased vulnerability of small families without an attendant boar (a relatively rare occurrence) was demonstrated when Prickett witnessed a hyaena seize a piglet that ignored its mother's warning grunt and tarried at the salt lick.

As with other pigs an alarm is greeted with a single urgent grunt followed by alert silence and immobility, after which there is a short flight or activity continues. When a hog is brought to bay by dogs it tries to back into the bushes or into a stump or bank and uttering deep grunts makes fast side slashes with its mouth open and sharp lower tusks exposed. Hunters with packs of dogs find giant hogs easy to hunt because they are bayed quickly and do not run far before being brought to bay again. Prickett (in lit.) has reported that wild dogs, *Lycaon*, formerly used to prey on hogs in the more open areas of the Aberdares.

Stockley (1952) describes shooting the adult male of a party that he came upon unexpectedly because it charged him and, on another occasion, after wounding a boar, he was brought to a halt by an outbreak of snorts in thick undergrowth followed by rushes which came within a few feet. These hidden bluff charges were kept up for 20 minutes. Few predators are likely to stand their ground against group charges and Soeberg (pers. comm.) has seen three hogs rush after a leopard, Prickett (1974) saw a mature male chase off a leopard which was stalking one of the piglets in his sounder.

The Yathabara records have confirmed that reproductive activity is continuous but that it follows a rather irregular pattern. This may have been influenced by the vicissitudes of the population which have already been discussed.

The incidence of single animals, which are usually fully adult males, generally peaks between February and May and this broadly corresponds with minimal records of pairs. The latter account for only a tenth of all groups at such times but marked increases in the numbers of pairs may follow a month or so after major peaks in the number of solitary animals. Since mating tends to take place in isolation, the frequency of groups of two (which are normally a male and a female) is some guide to breeding activity. Between 1970 and 1973 indications of mating peaks corresponded with the latter part of a rainy season and a decline in the incidence of single males but they did not follow a regular annual rhythm.

Courtship is rough and noisy. Once the boar has identified an oestrous female he keeps close to her, grunting and butting her hindquarters and flanks with snout or forehead until she finally stands and allows copulation which may last up to ten minutes. Stockley (1952) remarked that it looked as though the sow enjoyed being knocked about; in spite of the appearance of coercion the oestrous female might also be responding to male cues. It has been found that the preputial fluid of domestic boars, which is scented with muskone, elicits a "standing reflex" in oestrous sows; in this context the

frequent urination of dominant male giant hogs may have a reproductive function. Facial secretions might also be important since the glands are likely to be stimulated during the rough contacts of male with female. I have estimated that about two-thirds of the adult male population is in the company of females at any one time, but, as I remarked earlier, the Yathabara records have shown considerable fluctuations in the number of solitary animals (see chart). Sounders tend to contain one adult male and female but even where there is a tendency towards more than one adult female, those in oestrus are unlikely to go undetected and a reservoir of solitary males is in the offing whenever a boar neglects the rest of a sounder in order to mate.

Gestation has been reported to last 125 days. In spite of breeding being continuous one might expect to find evidence of more births following the mating peaks. Prickett (in lit.) has remarked on litters being more in evidence in July and August in some years but birth peaks tend to be masked by a combination of continuous breeding and heavy mortality of piglets before they start to be seen about with their mother.

Maberly (1963) reported hogs carrying grass to a retreat. Parturition is reported to occur in a dry spot under a fallen tree or similarly protected retreat. There may be two to eleven young. They are straw-coloured at first with no trace of stripes; the fur soon darkens to brown and then to black. The young accompany the adults almost immediately after birth and display behaviour that is reminiscent of certain antelopes when danger threatens. The sow makes a loud alarm grunt, whereupon the piglets lie absolutely flat and still, a subterfuge assisted by their colouring. If molested they squeal loudly, whereupon the sow or other members of the sounder charge or make intimidatory demonstrations with loud snorts.

Until they are about a week old, the mother remains in dense cover and Prickett (in lit.) writes

> "It appears that the sow brings them out of cover at about that age and for the next week or so they remain very much under her stomach, walking in line from chin to hind legs. Their ability to move in unison with the mother is most marked. On account of her low-slung belly little more than the row of tiny feet

can usually be seen. They have the habit of all sucking from the one teat which in consequence becomes elongated. The piglets play equally as much as wart-hog piglets but tend to chase less. They are more aggressive and fight by knocking noses for hours. It is probable that most piglets are taken by hyaena and leopard during such fighting and that when a single piglet survives it is because it then has no brothers to fight with and keeps closer to its mother.

Snout knocking is much more used in friendly bouts between juveniles. They start by pressing heads together then one lifts the snout upwards and tries to push the snout of the opponent to one side. If it succeeds then the opponent can no longer participate until the heads push together once more. In trying to avoid this happening the snouts go higher and higher until sometimes they can get them no higher and both automatically break free and start all over again. This can go on for quite a long time. There is no knocking together."

I have already discussed the relationship between skull structure and the prolonged contests of all the East African pigs (see p. 192). Snout knocking is predominantly a male activity and male competition evidently starts early. What is especially noteworthy is the occasional mass confrontation of immature pigs when two sounders meet and the boars begin to fight. At the same

time as the two adults are charging or pushing one another the younger pigs engage in snout knocking and it is interesting that there is also a massed pursuit of the vanquished male by a noisy rabble of youngsters. This reinforcement of a rout is also typical of the mobbing and exploratory behaviour of young males. Young hogs are inquisitive and Prickett has described them moving closer to an object of inspection by definite stages and any sign of a retreat is followed by a chase.

Females are probably able to breed at one year and males may remain in the mother's sounder longer, gradually tolerated less and less by the adult males as their secondary sexual characteristics, most noticeably their face glands and cheek plates, develop.

The species has not done well in captivity, possibly because of ignorance of its feeding habits and apparent need for quantities of mineralized earth; nonetheless *Hylochoerus* is a promising animal for domestication. The principal advantages are that it is a grazer and less of a rootler than *Sus*. Growth rates are probably below those of domestic pigs but the meat is lean and of excellent quality. Captives appear to be tractable and easily tamed. I believe the potential contribution of this species to protein needs in the tropics should be investigated.

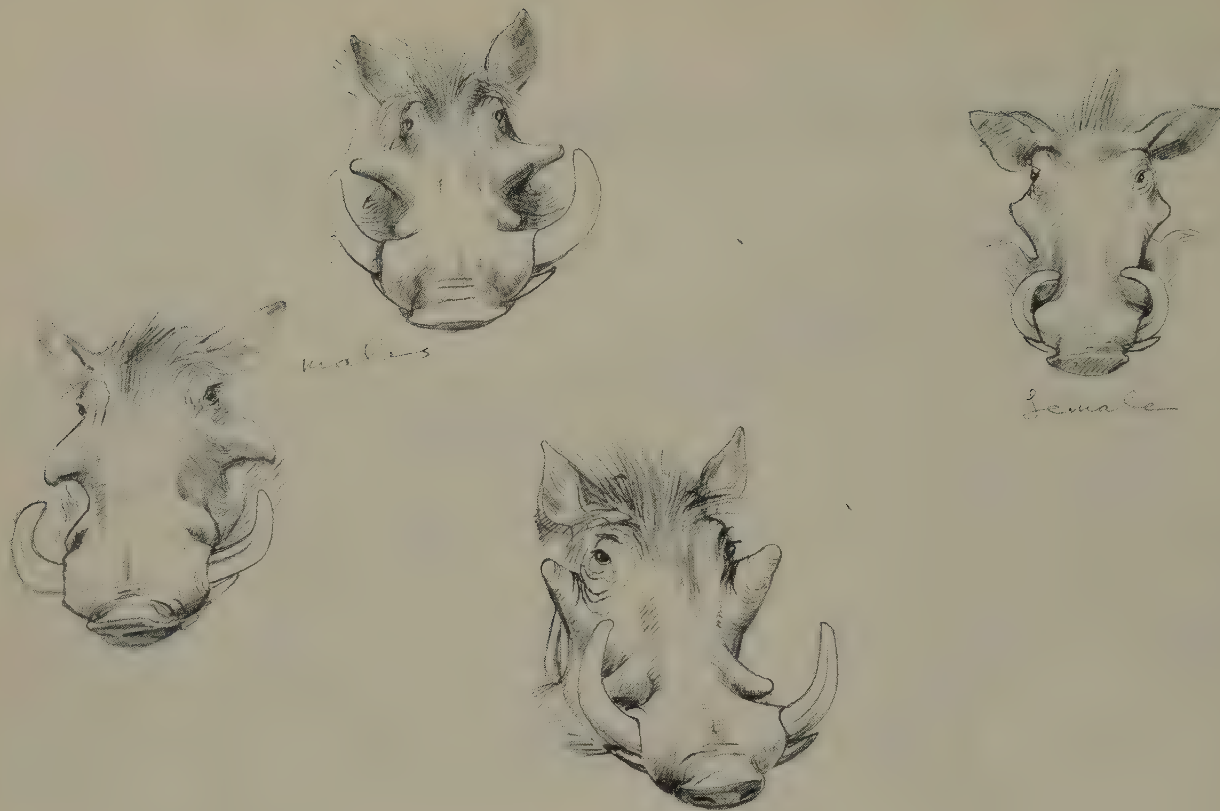
Warthog
(Phacochoerus aethiopicus)

Family Suidae
Order Artiodactyla
Local names
Mbango, Ngiri (Kiswahili), Ezo (Madi), Ng'gii (Kinyaturu), Meseyiandet (Kisebei), Kul (Lwo), Eputir (Karamojong), Ngele (Kinyiramba), Njili (Kizigua), Ingili (Luhya), Njii (Kikamba), Eputiri (Ateso), Butiei (Kalenjin), Lbitt (Samburu), Putuyandi (Kidorobo), Ol bitir (Masai), Dofar, Karkari (Somali), Aluf (Arabic).

Measurements
head and body
125—152 cm males
105—138 cm females
height
65—84 cm
tail
38—50 cm
weight
85 (68—143) kg males
57 (48—75) kg females
Average biomass weight
80 kg

Warthog
(Phacochoerus aethiopicus)

The warthog is often described as an ugly animal, yet if we used the sort of criteria that are employed to judge the merit of a piece of complex agricultural equipment or a machine of war, even our aesthetic judgement of the warthog might be modified; this mechanistic and functional approach was employed in the comparisons of pigs in the suid profile (p. 184), where I pointed out that the disproportion of the pig's head in relation to the body is due to the use of its head as a lever for food and as a weapon in trials of power and weight between individuals.

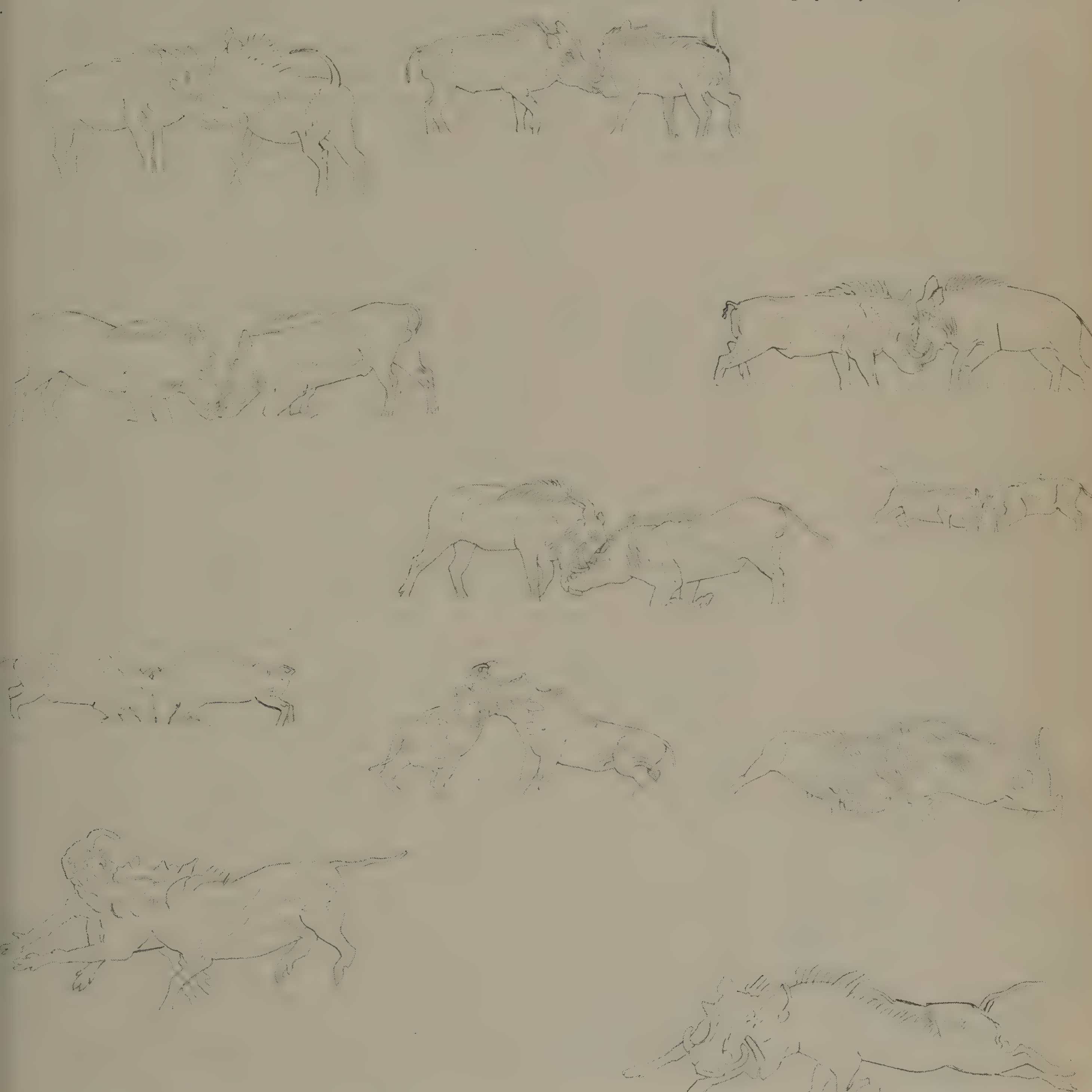


Individual and sexual differences in the shape of the "warts" and the flare of the tusks.

The warts from which this pig gets its name are comparable to the pads worn by American footballers. In the male they consist of three paired masses of dense connective tissue; the female dispenses with the snout warts and her protuberances are altogether less extreme. These warts are disposed in such a way as to protect the eyes and jaws from the hammer-like punches that contestants exchange during highly ritualized head duels. Their massive curved tusks might be described as snout antlers since they engage one another in head-on tusk to tusk and forehead to forehead pushing contests. The animals may engage from close quarters or they may charge into one another. The pushing is interrupted by lightning disengagements to thump at the side of each other's faces; these efforts are usually parried but the low sideways blows are violent and fights are often bloody (see illustrations opposite). Jaws and skulls quite frequently show signs of healed fractures and Monfort (1974) reports deaths from fighting in Akagera. On the rare occasions in which a warthog retaliates against a predator or human it employs the typical suid slashes with a sharp lower tusk, yet these slashes are not normally used in ritual fights, which end in the weaker animal turning tail, in which case he is not pursued far. Perhaps fatalities tend to be the result of equally matched rivals resorting to all-out fighting when the out-

come has not been resolved in the usual ritualized contest. Even young pigs spar with one another and adult males make spontaneous onslaughts on shrubs and tussocks. Females have less widely flared tusks and are less well protected by their smaller warts and are altogether less heavily built. Nonetheless, they also spar with other females occasionally.

Male warthogs fighting. (From photographs by H. Kruuk.)



Warthogs are longer in the leg than most pigs and they trot with a springy long stride and straight back, a gait that is quite unlike the clumsy and probably energy-consuming gallop of the bushpig, in which the back is repeatedly flexed and the limbs at front and back are closely synchronized. Warthogs are surprisingly fast and, although they are usually close to a bolt-hole, are capable of sustaining a rapid pace for a kilometre or more. The lengthening of the legs increases the distance between the head and the ground; instead of elongating the neck or snout the warthog has got round this problem by dropping on to its knees to feed and it will even move along, grazing and scraping as it goes, without rising to its feet. Kneeling is a built-in behaviour pattern and even newborn piglets kneel to feed. However, it is not only the behaviour that is inborn, because the callosities characteristic of carpal joints of the warthog's forelegs are present on embryos. This phenomenon has excited some discussion and Waddington (1953) has pointed out that even before the trait was hereditary selection would have favoured populations with the most satisfactory capacity to develop callosities, and he suggested that a genetic change could eventually occur "which will modify some other nearby region of the embryo in such a way that it takes over the function of the external pressure interacting with the skin so as to 'pull the trigger' and set off the development of the callosities". Other examples of such "anticipatory" adaptation are the dental "wear" patterns in the dugong and the rodent *Uranomys* (see Volume 11, p. 652).

Apart from sexual differences, warthogs show a great deal of individual variation. This gave rise to the naming of numerous sub-species in the past but the names have no consistent correspondence with regional populations, although there are some size gradients. However, these and other characteristics might equally well be a response to diet and other environmental factors.

The warthog is distributed throughout the savanna grasslands and open woodlands of Africa and generally belongs to a community that includes *Orycteropus*. High densities of warthogs are probably assisted by an abundance of *Orycteropus* holes and a deep burrow is essential for protection from predators as well as from fluctuations in temperature and humidity. The young are particularly vulnerable to cold or damp and burrows must be equally crucial for the adults that live in the Shira Plateau, 3,000 m up Mt Kilimanjaro. Warthogs have no insulation from fur or subcutaneous fat and Cumming (1975) reported hogs of 8 to 10 months dying of cold when exposed to night temperatures of 0°C, a vulnerability that contrasts strongly with forest hogs or bushpigs that live at high altitudes without needing a shelter. Young bushpigs maintain almost even temperatures in the course of a day, whilst young warthogs under the same conditions rise from 34° to 37·5°C (Sowls and Phelps, 1966). Cumming has recorded even greater changes of rectal temperature in adults with a total range of nearly 7°C in the females he measured, which reinforces suggestions that the shelter of holes is essential for physiological reasons. Temperatures within burrows have been recorded as ranging between 16° and 30°C. Being diurnal, the warthog is often exposed to excessive heat and will seek shelter from the sun by going into shade or by wallowing in mud, a practice that is commonest in the dry season. On the other hand, families get into a huddle or lie on top

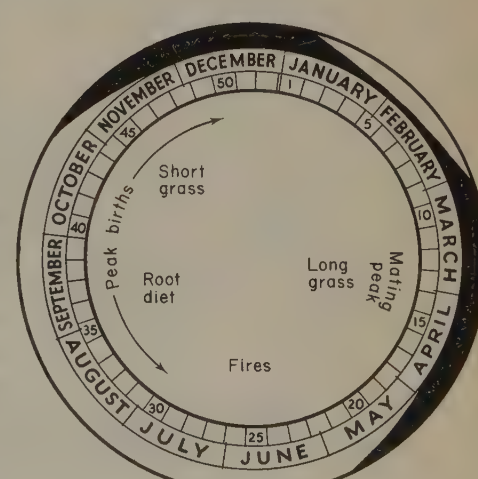
of one another on cold days and individuals will bask in sunlight after emerging from their holes.

Warthogs can dig adequately, sometimes scraping earth with their forefeet but mostly excavating and pushing earth with their snouts and tossing it out with a spade-like motion of their heads, but only in areas devoid of *Orycteropus* do they need to do much more than modify existent holes or crevices. The use of subterranean shelters by ancestral *Phacochoerus* was presumably dependent in the first place on an abundance of *Orycteropus* holes, and even today these can be very numerous indeed in undisturbed areas. Cumming counted 57 holes per sq km in the deciduous woodlands of North-western Rhodesia. Such an abundance of holes allows hogs to circulate and they do not stick to one burrow for more than a week or so at a time. Nonetheless, Cumming's exhaustive data* on the warthog's use of holes showed that they have favourite holes, which are generally large and durable and that these are well spaced out. Furthermore, the intensity of use corresponds with the spatial distribution of recognizable population units, which Cumming calls clans.*

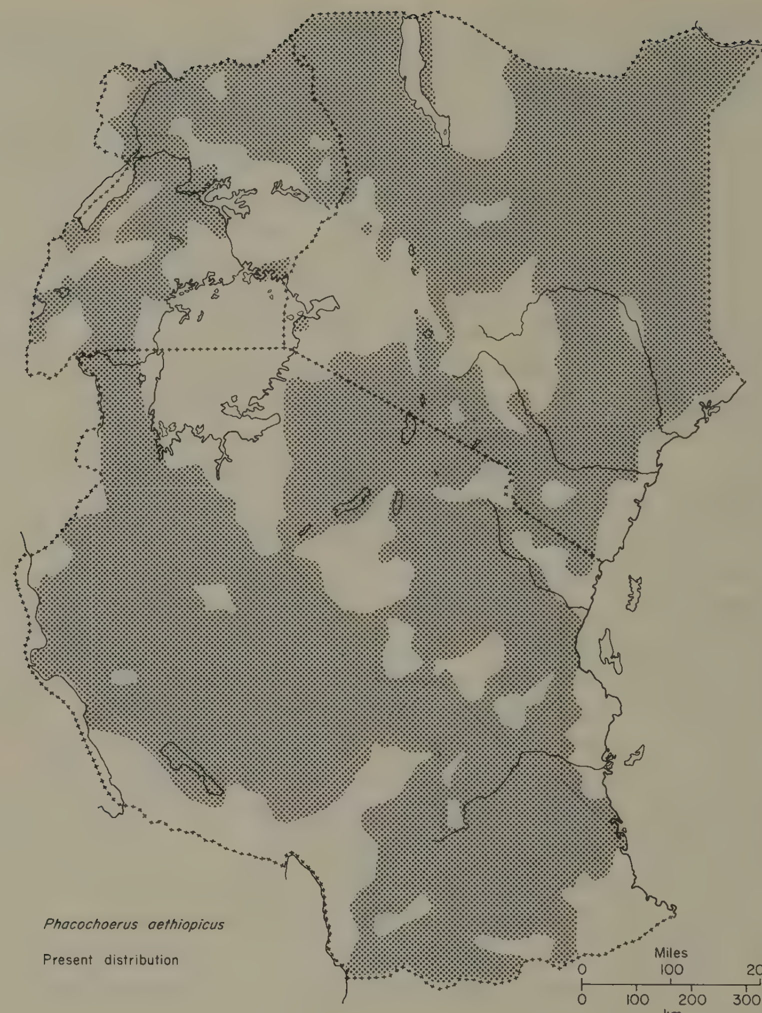
Although warthogs are generally sedentary, Bigourdain (1948) recorded populations in Senegal that vacated their wet season range to converge on rivers during drought. Sedentary habits are made possible by the warthog's ability to use a particularly nutritious source of food during the driest period of the year. In the fire-climax savannas, the period following the fires is generally a time of food shortage because few animals can get at the remaining portions of the vegetation that are underground; yet, in some habitats grass rhizomes and stem bases would probably exceed the 2–5 tons per hectare estimated by Cumming. Not only are leaf bases and rhizomes a bulk source of food, but they are also a store for concentrated nutrients that are available in that form only during the dry season. The warthog is able to unearth roots and rhizomes with the sharp edge of the rhinarium, making a shallow spade-like scoop even in the hardest of soils and is able, therefore, to enjoy a food that is only shared with some subterranean insects and rodents and the occasional rhino or elephant.

The presence of several genera of phacochoerine pigs in the East African Pleistocene (see p. 185) implies that open-country pigs were a diverse and well established group. The modern warthog, instead, only becomes numerous in the Upper Pleistocene. All the evidence suggests that the role of fire became much more important towards the end of the Pleistocene and it is possible that this factor may have favoured the warthog. The extinction of numerous related pigs may have allowed the living warthog to expand its ecological niche to enjoy a wider range of habitats today than its ancestors did in the mid-Pleistocene. It is significant that the numbers of warthogs recorded during game counts in Akagera remained much the same whether the grass was burnt or not (Monfort, 1974). The contemporary presence of warthogs in some favourable habitats could be seen as an expansion into empty suid niches. Guiraud (1948) reported warthogs living a nocturnal life in densely forested areas of West Africa and I have seen adult males grazing alongside giant hogs at 2,300 m in the Aberdares at 10 p.m. on a cool night.

Warthog calendar.



*Cumming's 16 year study of the ecology and behaviour of the warthog (1975) is a primary source of data on this species and his work should be consulted by anyone in search of further information on these pigs.



Notwithstanding these observations and other evidence of a wide range of habitats, the warthog is an animal that is primarily adapted to feed on short perennial grasses and is commonest on alluvial soils in lightly wooded country with a mosaic of vegetation types, preferably laced by numerous drainage lines or grassy glades. Warthogs in the drier parts of Tanzania and Uganda feed on the bases and rhizomes of grasses as well as on the occasional shrub roots during the dry season but graze when the green flushes arrive. In Central Tanzania, where warthogs are most numerous on the hardpans and open margins of *mbugas* during the dry season, their favoured foods have been recorded as the roots and rhizomes of *Panicum maximum* and *Cyperus leucocephalus* as well as the roots of *Commiphora* spp. and of *Lannea* (Harrison, 1936). In Upemba, Verheyen (1951) noted *Hyparrhenia* roots, while in the woodlands of north-western Rhodesia Cumming found them feeding mainly on the rhizomes of a species of couch grass, *Digitaria milanjiana* and *Tristachya superba* during the dry season and turning to grazing in the rains. During the brief seeding period at the end of the rains he watched them stripping seeds by dragging grass heads through the mouth from side to side.

Bradley (1968) noted that Nairobi Park animals turned to eating long green grass in preference to short dead grass at the end of the dry season.

All observers have noted that warthogs are highly selective in their feeding habits. In West Uganda, Field (1970c) found warthogs three times as numerous in areas where their favourite grass, *Sporobolus homblei*, was common in large monospecific mats. The most favoured species are tufted perennials that have been kept short by heavy grazing or fire and the growth form of the grass may be significant in their choice of grazing. The following grasses have been recorded as major foods in East Africa.

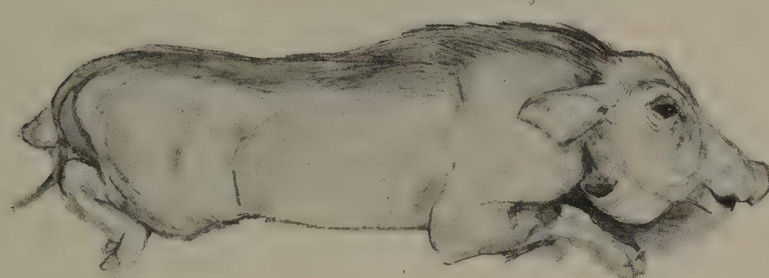
W. UGANDA (Field, 1970c)	N. TANZANIA (Lamprey, 1963)	S. KENYA (Frädrich, 1965)
Sporobolus spp.	*Bothriochloa* spp.	*Sporobolus pellucida*
Microchloa kunthii	*Cenchrus*	*Eragrostis tenuifolia*
Brachiaria	*Panicum maximum*	*Harpachne schimperi*
Cynodon dactylon	*Cynodon dactylon*	*Cynodon dactylon*
Chrysochloa orientalis		*Digitaria macrobole*

The fruits of *Balanites, Sclerocarya, Ficus*, mangoes and other fruits are occasionally eaten. Recycling may be important, as young warthogs regularly eat their mothers' faeces and Field saw dung eaten rather frequently by an older male. Bradley (1968) saw them eating rhino dung and dirt. Young pigs in zoos are believed to avoid constipation as long as they eat some earth. Earthworms are reported to be commonly eaten during the wet season in Tanzania (Balson, pers. comm.); scorpions, centipedes and larvae are reported (Krumbiegel, 1954, in Frädrich, 1965) and in drought they may nibble the meat or bones of dead animals. They are sometimes destroyed as pests for raiding wheat, rice, beans or groundnut fields.

Like the hippo and forest hog, the warthog grazes with its hard, sharp-edged lips. It crops fresh short grass close to the ground with an inward short nod but longer or tougher grass may be taken between the teeth and torn up with a forward wrench. Grasses may be selected by scent for Field saw his tame warthog take *Ocimum*, a distasteful aromatic herb that was generally avoided, but once plucked it was usually rejected on taste.

Warthogs are evidently capable of managing on rather little water as they live in much drier habitats than any other pig species. Nonetheless, they are generally found within walking distance of water and they drink once a day whenever this is possible; they often drink after the hottest time of the day but this activity varies from place to place. They may accompany herds of impala, waterbuck or zebra, possibly enhancing their security thereby. Depending on the season and class of animal, hogs may feed throughout the day but most intensively in the morning and evening. Feeding may continue into the first hour or so of the night and adult males may be less dependent on holes and simply lie up in cover for part of the night. In some areas, particularly where they suffer intense persecution from human beings, warthogs may take to feeding at night. They may emerge from their holes before sunrise but in weather that is both wet and cold the mother and young may delay their emergence. After an intensive feeding period in the early

mornings, warthogs become less active and rest in the middle of the day, becoming active again in the afternoon and feeding continuously in the late evening. They spend more time resting in the shade on hot days and also wallow more frequently during hot weather. Captive animals deprived of wallows have been reported to develop cracks in the skin and the activity is necessary for the animal's health. Buffalo and elephant wallows or even piles of earth excavated by *Orycteropus* or mole rats may be rolled in but warthogs will also dig their own wallows or use temporary puddles after rain. In fact, token digging often precedes lying down. Hogs always sink to the knees before lying down and get up hind first but an alert posture, sitting on the haunches, is sometimes adopted.



Warthogs are very alert animals and a small party of grey pigs breaking cover is a familiar sight, their manes bristling, heads as erect as their short necks will allow and tails vertical with the tassel waggling like a small black flag on top as they trot away. Speeds can approach 55 km per hour. An intruder is likely to be identified first by smell, if the wind is right, or by hearing in grass or scrub. Sight is important in open habitats and at closer quarters but they respond less to visual clues and are easier to stalk than most antelopes. When pursued, they try to run for a burrow, which all but the youngest pigs enter backwards. They cannot check the holes in advance, so that when an individual catapults out again this is often due to earlier occupants. In urgent circumstances scent may be the main guide to occupancy of holes; a warthog may approach an already occupied hole with the obvious intention of entering, only to stop and sniff the ground some yards from the hole and then move off, which suggests that hole-use might operate on a "first come, first served" basis. Warthogs inspect holes in the course of a day's movement about their range and thus learn which holes are free.

Glandular scent marking is a formalized activity and Cumming (1975) has described their behaviour: "Warthogs twist the head to one side and the inner surface of the lip flange, lying behind the tusks, is wiped against a tree or stump. They then move forward and methodically rub the pre-orbital area on the marked object. The chin, neck and sometimes the trunk may also be rubbed. Marking was seen in the vicinity of holes, wallows and throughout the home range." Like dogs, the pigs inspect recently placed marks and then place their own mark on top and Cumming noted particularly frequent

marking behaviour in a recently mature male during his first rutting season. This hand-reared but free-ranging animal would make periodical visits, going from one marking post to the next, inspecting and marking posts which eventually became worn by abrasion. The mark is generally placed as high as the animal can reach. I have seen a male warthog deliberately walk up to a female with piglets and place his nose under her chin. He then started to nod gently, which slid her rhinarium and chin up and down the bridge of his nose. This action might have transferred saliva or scent from her mouth and chin but it certainly forced her to smell his face. It is possible that this clumsy sliding was actually marking her with both orbital and salivary secretions. Although the female had given signs of wanting to flee as he approached, she appeared to relax after this performance and the two then grazed in company for a couple of hours.

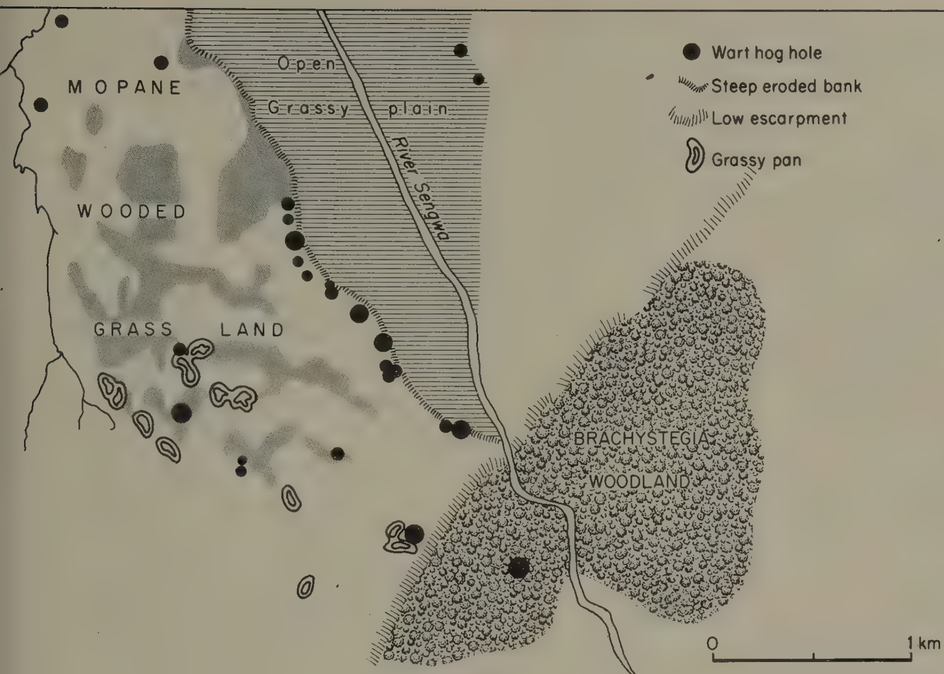
All greetings between pigs involve nose to nose sniffing and they pay particular attention to the corners of the mouth and eyes, often rubbing one another's pre-orbital areas in pacific encounters. Scent obviously plays a very important part in their social life and may be an integral part of the spacing out of individuals and populations.

Warthog society appears to be organized at several different levels. Females segregate themselves to have their litters but even after the young are able to accompany their mother the family may remain a single social unit or sounder. More commonly, however, the female joins up with other females and their young. That such families are probably closely related is suggested by Bradley's observation (1968) of two yearling youngsters both getting pregnant simultaneously. After having separated to give birth, they joined up again a month later to form one matriarchal group and an examination of the age and class structure of other Nairobi Park sounders fitted this pattern in the majority of cases.

Mother and young families are not the only units. Sexually active males tend to wander quite freely on their own and always sleep in separate holes and non-breeding males form bachelor groups that are present throughout the year but are more conspicuous outside the breeding season. Females are only temporarily on their own at farrowing time and subadult mixed groups have generally been chased off by their mother. The sounders studied by Cumming at Sengwa were recorded ranging over areas between 64 and 374 ha. Two or more sounders might share all the resources in an area and the boundaries often showed a rather close correspondence in spite of individual groups tending to have distinct core areas. Sounders with overlapping ranges kept apart while foraging, always slept in separate holes and only met briefly near wallows or water holes.

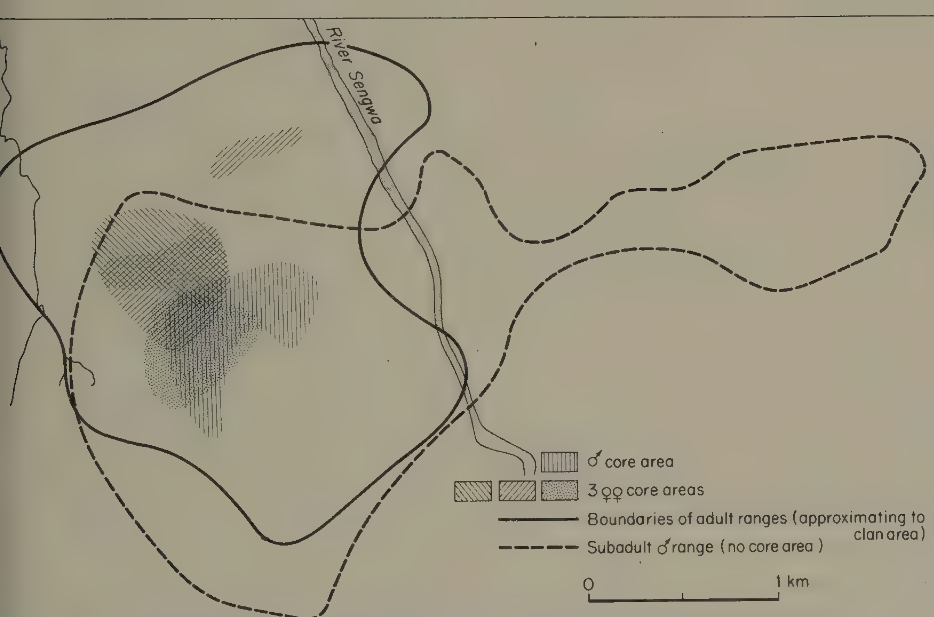
Considering the attachment that animals have for their home area and because various sexual groupings are involved, it is likely that most of the pigs sharing a common range have a blood relationship in spite of the sounders generally avoiding one another.

By plotting the movement of most of the warthogs in the vicinity of the Sengwa research station, Cumming found more or less consistent groupings of sounders in what he called clan areas, each averaging about 4 sq km. Within these confines sounders slept in separate holes and some sounders had favourite or core areas but a certain amount of circulation meant that



Above left: Topography of a warthog habitat on the Sengwa river. (From Cumming, 1975.)

Above right: Clan boundaries at Sengwa, shown in relation to holes used for shelter. (After Cumming, 1975.)



Home ranges of five representative members of a warthog "clan".

no hole could be regarded as the prerogative of any sounder or individual. There was minimal contact between animals coming from different clan areas and the avoidance that typifies inter-sounder relations is even more marked between clans, but the question of whether clan areas can be termed group territories remains uncertain. Monfort (1974) describes males fighting when one approached another that was with a family but Kruuk (pers. comm.)

Silhouette of warthog in "proud" posture.

saw two fighting each other on their own and in an open plain. In the absence of background knowledge it is not possible to know whether such fights are between members of different clans or simply intolerant individuals during the rut.

Clashes usually involve the convergence of separate parties or individuals on a single resource. This may be a female attracting more than one male or a burrow, water or a wallow where competition can arise between independent members of both sexes. Bradley thought that each pig seemed to defend a small circle around itself and he noted that female clashes were commonest over holes (particularly after rain had fallen) and that all pregnant females became intolerant shortly before giving birth. A male trotting up to another which is already with a female or females almost invariably provokes a stereotyped display but confrontations do not always concern a female. Both animals approach one another with head and mane erect and a prancing stiff gait. They deflect their paths for a moment to present their profiles in a lateral display with mane fully erect. One may then rush forward and an intruder very often breaks away at this point but, if he stands his ground, snouts and tusks clash together and there is a contest (see page 233). If one animal is knocked off balance or is continually pushed back, he may eventually sink into a lower defensive position with flattened mane and start to squeal, breaking away as soon as he can. The victor seldom pursues with any vigour or for any distance and fighting scars are not often seen on the bodies of warthogs, although heads may be well bloodied. A direct trial of strength and weight is the main criterion of rank in many ungulates but in the warthog's case, open country dwelling might have increased the value of visual cues, hence the frequent lateral displays and the avoiding action of smaller animals. In this connection it is interesting that tuskless subadult pigs have white hair tufts on the lower jaw warts, which are very passable imitations of tusks, particularly when viewed head-on. Such pseudo-tusks might help intimidate other youngsters, and the social advantages of a hierarchy, even at this early age, might have encouraged the evolution of this curious juvenile characteristic.

Young warthogs spend a great deal of time threatening one another, displaying and engaging in clashes that are generally described as play. In two captive litters of my own acquaintance, definite dominance hierarchies were established between the siblings at a very early age and it is possible that dominance and subordination are continuously tested almost from birth in every encounter. The greetings mentioned earlier almost always imply submission in one or other of the participants even when they are long established female companions within a sounder, and the ritual of the ceremony does not altogether hide the elements of appeasement. For example, two females that know one another well may approach each other slowly with outstretched heads and flat manes. They sniff at one another's mouth and eyes and may then proceed to nibble the neck and mane, which seems to be the preferred area for social grooming. Any excitement causes the mane to bristle but this is intimidating, whereas it is appeasing in function when presented limp on a lowered neck. When one partner grooms another one's neck, the first action is a gentle massage with the snout and then nibbling or combing of the hair through the lower incisors. Falling over, the groomed animal may then invite attention to its belly by raising the legs.

Humans are commonly solicited by captives in this way and Frädrich (1965) describes a tame warthog visiting the pen of three young elephants and lying down in front of them so as to be touched by them.

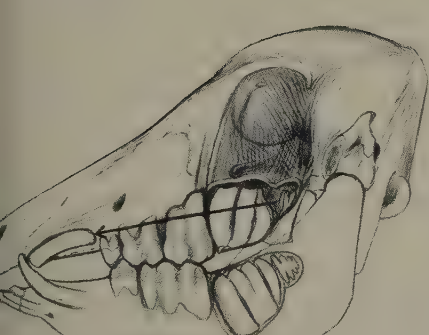
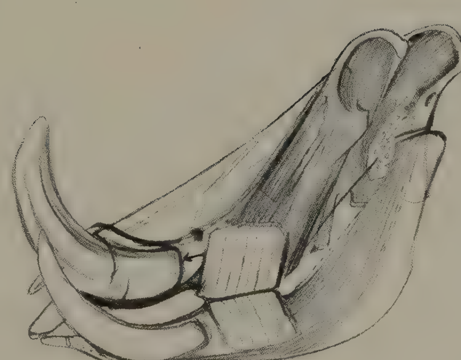
Exposure of the belly is a common element in the appeasement behaviour of many species and this might also explain Henshaw's (1972) observation of an adult male warthog falling on to his side with two legs held stiffly in the air when approached by a very large herd of buffaloes. The pig remained motionless for four minutes while the buffaloes passed closely by on either side; curiously enough, a female and two juvenile pigs accompanying this male ignored the buffaloes and continued to feed. However aberrant this male's behaviour, the difference in his reaction might imply that hierarchical relations play a more compelling role in male society. Male intolerance might be a seasonal phenomenon as parties of males, including large adults, tend to come together during the dry season. The incentive for such gatherings seems to be the short grass lawns where there is green grass and rhizomes to eat and their monosexual nature is undoubtedly influenced by the fact that females are generally farrowing at this time. Bradley's suggestion that females drive the males off is unlikely, as males are nearly always dominant and only show an interest in females in the breeding season; the short grass areas are also a preferred habitat. Greater tolerance of other males outside the mating season might have a physiological base and it is interesting that Child *et al.* (1968) recorded seasonal fluctuations in the weight of the testes and the level of spermatogenesis in warthogs in Rhodesia. So far as females are concerned an annual cycle is assisted by the fact that females do not ovulate while lactating (Clough, 1969).

In eastern and central Africa south of the equator, the young tend to be born between September and December, at the end of the dry season or the beginning of the rains. In equatorial Uganda newly born young have been recorded during the dry seasons between December and March and again between June and August but there is some breeding throughout the year. All mating peaks have a similar timing in that they occur four or five months after the breaking of the rains, when both sexes are presumably in peak condition. The timing of births is likely to subject the young to a high level of predation, but dry burrows and later fresh green grass for the young may be an advantage that outweighs vulnerability to predators. Bradley has suggested that humidity in the burrows may tend to get too high at the peak of the rains and that flooding of the burrows may be a factor of some importance locally.

Cumming has described males visiting the holes of oestrous females in the early morning and chasing off young males and bachelor groups if they emerged; he suggested that males probably follow up oestrous females from their holes. He only captured an adult male in the same hole as mature females on three occasions out of over 100 captures but once saw a couple emerging from a hole and mating without any preliminaries. In the Nairobi Park, Bradley (1968) found that some groups and individuals wandered about more than others. One male traversed the entire range of the female groups in his study area and a female could have been served by four different males. In this area there were forty adult females distributed in twenty-four matriarchal groups with only ten regular adult males and five occasional

Above and right: Surface drawing and dissection of juvenile warthog piglet.

Bottom right: Skulls of juvenile and old adult warthog showing tooth succession and forward movement of M^3. Zygomatic arch and mandibular process cut away.


visitors to serve this large number of females. In spite of this he thought that the maximum fertility rate was achieved. A very large sample of warthogs shot in Rhodesia revealed that 72% of the adult female population achieved pregnancy.

The courting ritual of these pigs is sometimes a drawnout affair. Clough and Hassam (1970) noted that one adult female urinated up to ten times as frequently as a male. Even after repeated attempts at mounting, a male will immediately transfer his attention to a female's urine and after smelling it he may leave that female abruptly and go off on his own. If a female is in oestrus a male then squirts a few sprays of his own urine over her deposit. Although urine deposits can be smelled by the male from some distance, a female's hunched posture also advertises the act and attracts the male's attention. Having identified her condition, the male may then pursue the oestrous female, which gives every indication of fear, defaecating loose excrement as she runs in a wide circle. The male, meanwhile, raises his mane and champs his jaws, salivating copiously as he does so and mumbling in his throat. The rhythmic opening and closing of the mouth and rhythmic grumbling combine to produce a chugging noise that has been likened to a "piki-piki" or motorcycle. Eventually the female slows down and at this stage the male falls silent and starts to massage the female's rump, which induces her to stand still with her ears back. She backs eventually into the male and he mounts her, jerking his head as he does so. Copulation can last for about 10 minutes. Simpson (1964) saw a young male preceding his approach by a circling movement with occasional spasms or shudders of the body and after several such displays he walked up to her and rested his chin on her rump without any chasing.

Signs of oestrus noted by Simpson are dark fluid stains down the female's hindquarters and an enlarged vulva. Clough and Hassam (1970) established that the oestrus period can last 72 hours with an interval of six weeks.

Gestation lasts nearly six months (170–175 days). Although the female has only four mammae there are records of up to eight young, but litters average two or three young. Grass has been found in some excavated burrows but newly-born young have also been dug out of unlined holes. Males have been seen carrying mouthfuls of grass down their holes in cold weather in Rhodesia, suggesting that such lining may be related to temperature.

Before birth the female secludes herself and drives off her former young and all other intruders. After giving birth the female will come out during the day to feed and rest. She visits the young down the burrow for variable periods from a few minutes to some hours at a time. At birth the young have a fairly thick covering of fine hair with just a trace of longitudinal stripes and white whiskers fringing the jaws. They are born fully active but are very sensitive to temperature and Bradley (1972) established that there are stable temperatures in the burrow even when violent fluctuations occur outside. The preferred temperature is about 20°C. At first the piglets remain in the burrow and the mother returns two or three times a day to suckle them. About two weeks after birth the young emerge into the open for the first time. They are extremely timid and rush down the hole at the least alarm. The length of the lactation period may vary; Child *et al.* (1968) estimated about 70 days but Cumming (1975) recorded a tame but free-ranging female

lactating for 151 days. They start eating grass almost at once and also eat their mother's dung. Some time between the ages of six and eight weeks they begin to follow the mother on forays, often together with another family, with which they mix freely. Like all piglets they try to maintain close physical contact with the mother's legs when they first accompany her and on hot days they keep in her shadow.

When a group is on the move, the largest female generally determines the direction the party will take and every activity, even defaecation, is closely co-ordinated in a family group. The younger animals are most adventurous and explore energetically, taking a bite here and another there, as they bustle about but they rush back towards the adult animal if frightened and while still very young they may drop to the ground and freeze. They engage in much circular running with side slams to one another's head (which orphans will do against a clenched fist). These contests may be an early manifestation of hierarchy, as may be the teat order while suckling. When Cumming captured families, the mother always had as many functional mammae as young and when one of his captive piglets died, the teat it had always suckled from simply dried up within a few days, without being used by any of the remaining siblings. Monfort (1974) observed that each youngster also occupies a well defined position when the family walks in line. If one tries to overtake a sibling ahead of it, it is immediately driven back to its place with threatening grunts or an actual attack.

Growth rates probably vary in the wild under the influence of seasonal fluctuations in food and parasite infection. Roth (1965) found differences between artificially reared warthogs and wild ones, with the latter developing over a longer period. In the wild, subadults can be recognized by their poorly

developed warts, withers and testicles. The tusks begin to grow beyond the lip before they are one year old but are still very inconspicuous. These features are well developed by the time they are three to five years and fully mature. Sexual maturity is reached at about eighteen months, with the female about one month ahead of the male. When fully adult the warthog develops a cylindrical body, hollow back and a naked wrinkled skin.

Equal numbers of both sexes are born and this ratio was maintained in the Sengwa population up to the end of their first year. There were fluctuations from year to year in the proportion of males in the adult population, at Sengwa dropping as low as 34% and rising as high as 47·8%. Clough (in Spinage, 1972) estimated that there was 50% mortality in the first years of life, while Bradley (1968) concluded that only half the annual increment of Nairobi Park young reached the age of six months, whereas there was a 15·4% mortality among adults. Spinage (1972) plotted a survival curve for this species in Akagera with a hypothetical longevity of seventeen years, which was presumably derived from zoo records. He suggested that warthogs seldom achieve their potential life-span and the high reproductive rate is geared to a relatively short life cycle. After reviewing records from other areas of Africa, Cumming (1970) concluded that there was evidence for differential mortality and his own records showed a sharp decline in the numbers of males seen in the month following the rut. He often found males spending the night in slight depressions and in dense grass and he recorded a lion killing one in just such a situation.

The principal predators of warthogs are the lion, leopard and cheetah, and the former have been observed to ambush them at the entrance of their holes and, on several occasions, to actually dig them out exposing several metres of tunnel before seizing the occupant. In the Sengwa area, Cumming found that 57% of the lions' kills were warthogs, whereas these pigs only represented 10 to 20% of the prey species available. Not surprisingly, this level of predation led to a decline in the pig population during his period of study and he was able to correlate this decline with a rise in lion population that was due to a migration from a disturbed area nearby. In the Kruger Park, warthogs account for nearly 2½% of the lions' prey species and a somewhat larger proportion of the leopards'.

Hyaenas, which often come into close contact with warthogs, appear to attack them rather seldom and the two species have been seen resting under a tree together, actually touching one another. Deane (1962) describes the warthog as being the more aggressive animal during the day, but points out that hyaenas will kill the very same animal at night that displaced them during the day. He found it not unusual between visits, that a warren previously occupied by hyaenas should be taken over by warthogs and *vice versa*; he also saw two hyaena pups playing outside the warren take fright and dash down the nearest hole which was already occupied by two warthogs. They soon reappeared and after peering around cautiously, came out again, having come to no harm with the warthogs below.

Wild warthogs seldom defend themselves from predators but captives can be dangerous. Frädrich (1972) reported that a tame warthog in Duisberg Zoo killed his experienced keeper and that captive females are sometimes fierce in defence of their young, but Kruuk (1972) saw one stand with no

sign of aggression while a hyaena disembowelled her squealing youngster. Schaller also saw wild dogs kill an adult male which made no vigorous attempt to defend itself. On the other hand, Cowie (1966) reported two males standing their ground against sixteen wild dogs, which gave way. Stevenson-Hamilton (1947) reported a female driving a leopard up a tree when it attempted to catch one of her litter. A martial eagle, *Poliaomaetus bellicosus*, was seen to seize a piglet of about 3·5 kg and drop it five times from a height of over 3 metres.

Warthogs suffer from a variety of diseases, the most serious being rinderpest, from which large numbers have died in the past. They are also a reservoir for African swine fever, a fact that has led to warthog extermination campaigns in some farming areas but, as Plowright *et al.* (1969) point out, this arboviral disease is transmitted by ticks, particularly *Ornithodorus moubata* (which also parasitizes *Orycteropus*), and the maintenance of the virus in enzootic areas may not necessarily depend only on the continued presence of the wild mammalian hosts.

Although warthogs are incompatible with intensive stock rearing or agriculture and their range is declining, they remain an important and very interesting member of all large savanna mammal communities and are well represented in almost all East African national parks.

Hippopotamids

Hippopotamidae

The earliest origins of the hippopotamus are still unknown. Fossil hippopotamus teeth first appear in the East African Lower Miocene but the earliest cranium, of a relatively advanced hippo, is from the Late Miocene deposits at Lothagam. Their absence from the earliest fossil record may be because they were solitary forest animals, as the pigmy hippopotamus, *Choeropsis*, is today. Indeed, for this species there is no fossil history at all but, in spite of having reduced the number of its incisors, it conveniently illustrates other aspects of hippo evolution because the skull is relatively conservative and this animal's ecological niche is undoubtedly close to that of the ancestral hippopotami.

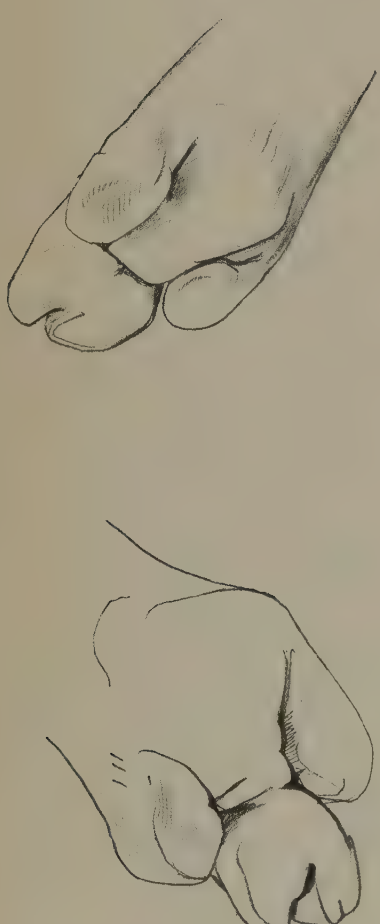
Hippos have resemblances with pigs, peccaries and anthracotheres and various authors have allied hippopotami more closely with one or other of these three groups. It is also possible that they evolved independently from a common suiform ancestor and that in this very early divergence they already tended to occupy the moister habitats. The pigmy hippo clearly represents a more conservative type than the Pliocene fossil forms; yet it is amphibious and its skin must have required a long period of adaptation to submersion in water or mud to be so highly specialized.

Among the abundance of Pliocene and Pleistocene hippos several were more lightly built than the present-day *Hippopotamus amphibius* and had longer limbs, but the softer, more herbaceous diets that are implied by low crowned teeth might have required more walking and greater agility without prejudice to their amphibious existence. Four functional toes with a wide splay and no protective hoofs could only have been retained by animals that were restricted to relatively soft ground.

The pigs' and hippos' common reliance on secure resting places might represent a carry-over from their origins as animals of the dense forest but the hippo's use of swamps and waters as refuges has allowed it to develop a peculiarly successful ecological strategy. The modest appetite of the hippopotamus is correlated with great economy in the expenditure of energy and a specialized digestion (see p. 182) and it is likely that all hippos shared these characteristics to some degree.

Hippos do not ruminate but they have a very slow rate of digestion and have evolved septa in the stomach and two accessory blind sacs that serve to direct and slow down the flow of food. Langer (1974) considered that at least one of these sacs might have developed before the mid-Eocene and that these structures developed independently from similar sacs found in the living peccaries, *Tayassu*.

These considerations are consistent with aquatic or semi-aquatic refuges having been an intrinsic element in hippopotamus evolution. Pressure from other herbivores and from predators might have pushed the earliest hippopotami into using swamps as retreats but it is likely that these refuges became the principal focus for intra-specific competition and that this can explain many of the extraordinary developments that are to be seen in the skulls of living and extinct hippopotami.



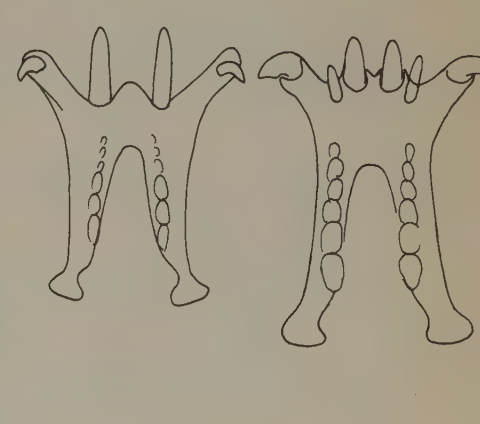
Left hindleg (upper); left foreleg (lower).

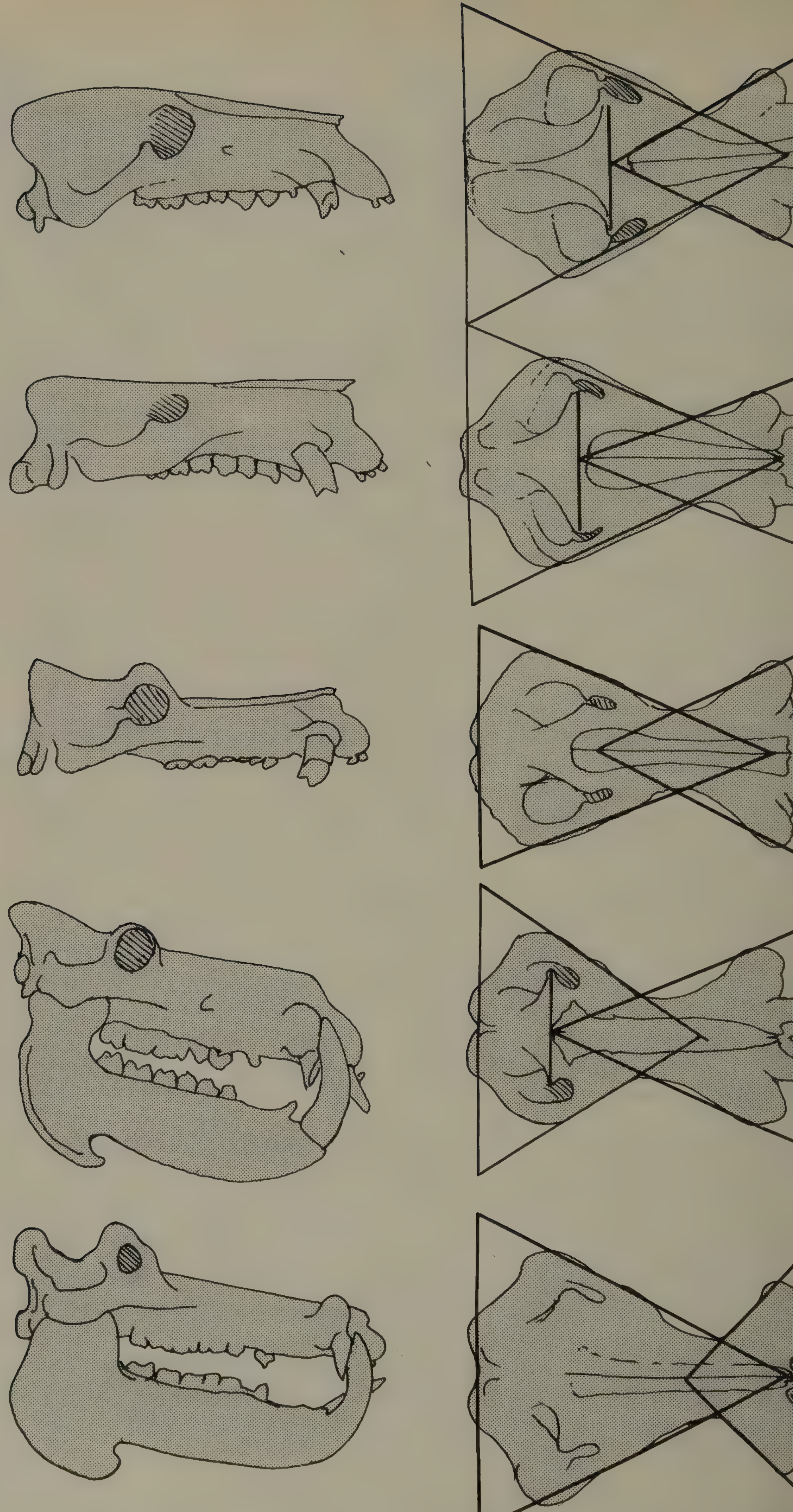
Immersion in mud or water would have put certain constraints on fighting that were not operative for pigs and peccaries. However, peccaries have remained the least specialized of suiformes and their relatively unritualized threat and fighting behaviour can conveniently exemplify a primitive condition. Fighting consists of simply using their canines in a wide-gaped bite while threats are an auditory and visual advertisement of the teeth by means of clashing of the jaws and "yawning".

With hippopotamid rivals partially or wholly immersed in water it is obvious that similar threats have to be made with the head raised so that the lower jaws come in to greater prominence during clashes. Bulky animals fighting in a medium where their movements are impeded must rely less on agility than on exactly parrying onslaughts and in a mouth-to-mouth contest this means that each animal must catch or hold the opponent's teeth with its own, after which the engagement becomes a trial of weight and strength.

In such a situation, the teeth at the front of the jaws cannot simply function as weapons of offence but must equally serve as a defensive barrier. To this end the teeth and lower jaw must increase in breadth, size and strength to carry the impact of stresses of clashing and pushing. As with the tines on antlers the exact arrangement of teeth is of less importance than the width of the jaw's span both vertically and horizontally. This is borne out by the fact that hippo jaws open to an astonishing wide angle and all hippo lineages show increasing distance between the canines across the front of the jaws but considerable variation in the number and orientation of incisors. Some species retained a full complement of six incisors in both jaws, "hexaprotodonts" and others reduced them to four, as in the living "tetraprotodont" *H. amphibius*, while the "diprotodont" *Choeropsis* has four incisors in the upper and two in the lower jaws (as do some variants of *H. amphibius*). The specialized *H. karumensis* lineage from the East Turkana Pleistocene had four tiny peg-like upper incisors and had reduced its lower canines while elaborating their bony sheaths and enlarging the two lower incisors so that the lower jaw became a huge four-pronged fork (see diagram).

Left: lower jaw of a highly aquatic "diprotodont" hippopotamus.
Right: lower jaw of *Hippopotamus amphibius*.





Choeropsis liberiensis

Lothagam hippopotamus
(Miocene—Pliocene boundary)

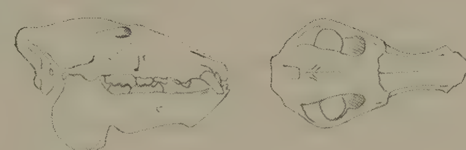
Hippopotamus protamphibius
(mid-Pliocene)

Hippopotamus amphibius

Hippopotamus gorgops (Pleistocene)

Comparing *Choeropsis* and the Mio-Pliocene hexaprotodont hippopotamus from Lothagam with later more advanced hippopotami there is a considerable increase in the span of the anterior teeth. By comparing outlines of these hippopotamus skulls with those of an unspecialized suimorph, the Oligocene peccary, *Perchoerus*, it becomes even clearer that progressive expansion of the anterior dentition and reorganization of the lower jaw and its articulation are dominant characteristics of hippopotamus evolution.

Perchoerus

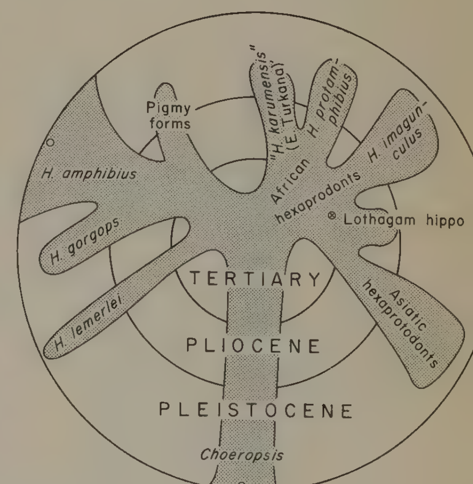


Merycopotamus dissimilis

Suggestions for a relationship between hippos and anthracotheres are largely founded upon striking resemblances in the anterior dentition and lower jaw of a Pliocene anthracothere, *Merycopotamus*, from India.

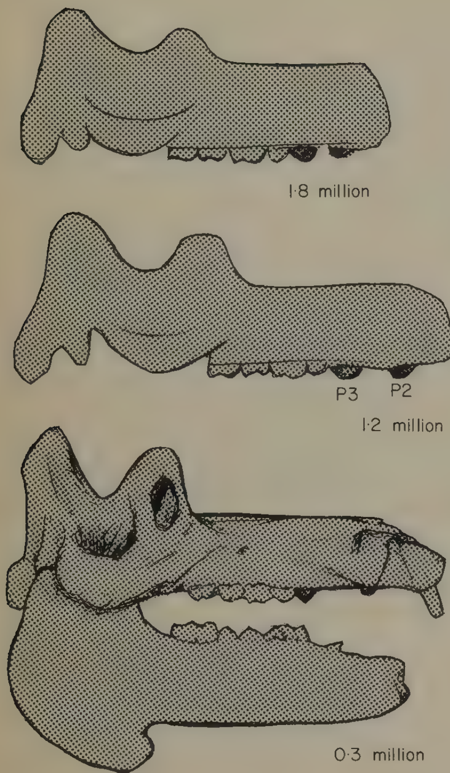
The temporal sequences of fossils suggest that anthracotheres may have occupied a semi-aquatic niche and were displaced by hippopotami as the latter moved out of their early forest niche and became larger (Coryndon, in press). The late date of *Merycopotamus* and various cranial features show that it is nowhere near the ancestry of hippopotamus and its resemblances are probably due to its occupation of a similar habitat and a convergence with hippos in its method of ritualized fighting. The very early hippos would have expanded their anterior teeth in a similar fashion and, in spite of its unrelatedness and in the absence of a true ancestor, *Merycopotamus* conveniently illustrates an early stage in the type of reorganization of the teeth and jaws that is so characteristic of hippopotami (see diagram).

The two contemporary species of hippopotamus differ in the degree to which the eyes have been elevated above the head and this is clearly an adaptation to more wholly aquatic habits. The two species are sympatric and it is clear that hippos were formerly able to exploit several distinct niches as four hippo species co-existed in the Lake Turkana basin during the Pleistocene (Coryndon, in press). Differences in the elevation of orbits imply adaptation to deeper water or more consistent immersion, differences in crown height imply more or less grass in the diet while considerable differences in size indicate different strategies in the use of resources. It is possible that the differing arrangements of the incisors and canines correspond with intensity or style of combat and might therefore reflect differences in social system. The existence of other hippopotamus species would have restricted the space available to any one species and densities would have been influenced by all the factors mentioned above. In a region of lakes and rivers with a wide variety of vegetation, the diversification of the hippopotami parallels that of pigs and bovids. It is clear that Pleistocene hippos must have had more restricted niches and that the modern hippo may have been free to



Radiation of Hippopotamidae (after Coryndon, in press).

Opposite page: crania of Hippopotamidae.



Evolution of *Hippopotamus gorgops* at Olduvai (after Coryndon, 1970).

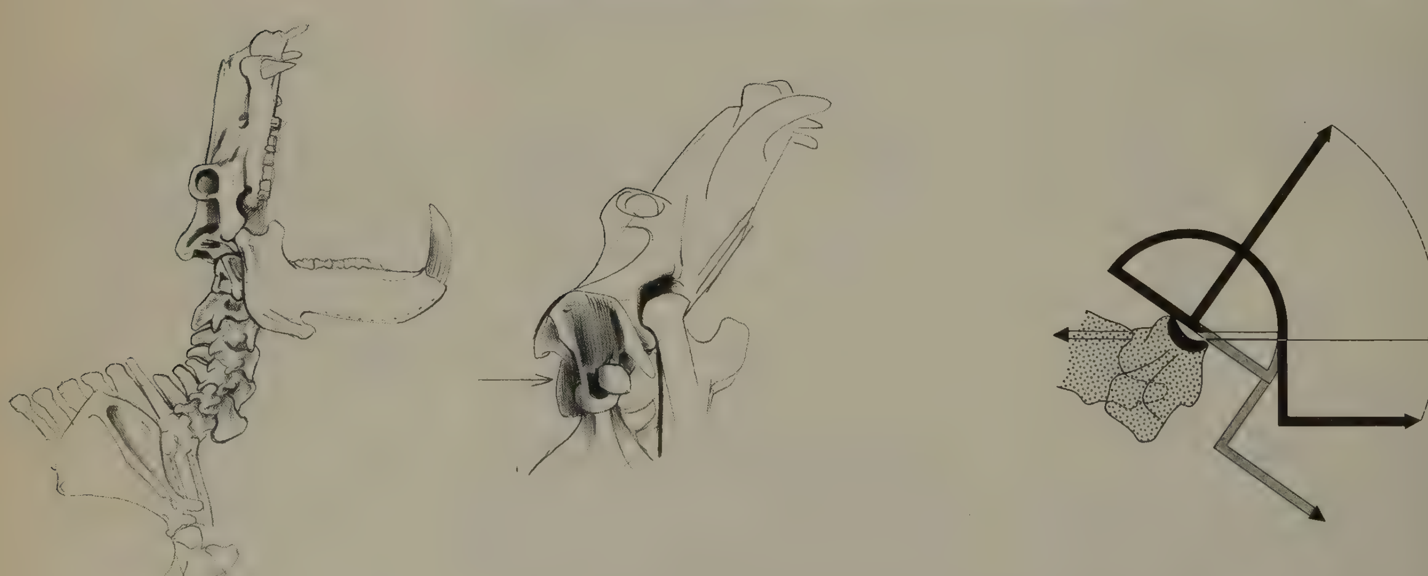
expand into habitats that were formerly denied to it. An early Pleistocene hippopotamus from Bed 1 at Olduvai is probably close to the ancestral line of *H. amphibius* but exhibits some features that anticipate the highly specialized late Pleistocene, *H. gorgops* (Coryndon, 1970). The Bed 2 Olduvai hippopotamus has a longer and shallower skull, more elevated orbits and a larger mandible but all these characteristics reach their most extreme development in *H. gorgops* in Bed 4. This species had such highly periscoped eyes that it must have been more aquatic in some important sense than other hippos. If fighting occurred with greater frequency in deeper water heads must have been elevated still higher during clashes than is generally the case in living hippos. The jaws were clearly capable of opening as widely or more widely than in *H. amphibius* and gaping contestants with their heads above the level of their bodies would have to take the main impact of clashes on the mandible alone. The vast lower jaw of *H. gorgops* is consistent with this interpretation. The mandibular condyle in hippos has migrated back so that the forces exerted by or against the lower jaw pass directly to the vertebral column. This arrangement is most exaggerated in *H. gorgops*, but all hippopotami have specialized the occipital region to accommodate to jaw clashing and "yawning".

Articulating on the axis, the entire cranium can jack-knife upwards over a wide arc of flexure while the heavy lower jaw is pulled down by exceptionally highly-developed digastric muscles (see below).

It is interesting that an aquatic rhinoceros, the Oligocene *Metamynodon* not only had hippopotamid proportions but had an enlarged prominent lower jaw.

The radiation of hippopotami during the Pliocene and Pleistocene was examined by Coryndon (1970, 1973, in press) and her scheme of hippopotamid evolution is shown on p. 253.

As more numerous and more complete fossils are discovered and as more is learnt about the biology of living hippopotami more precise correlations between form and function should become possible.



The articulations of the skull and lower jaw in relation to the cup of the first cervical vertebra.


A-R-C-H
weight
loose folds
block hea

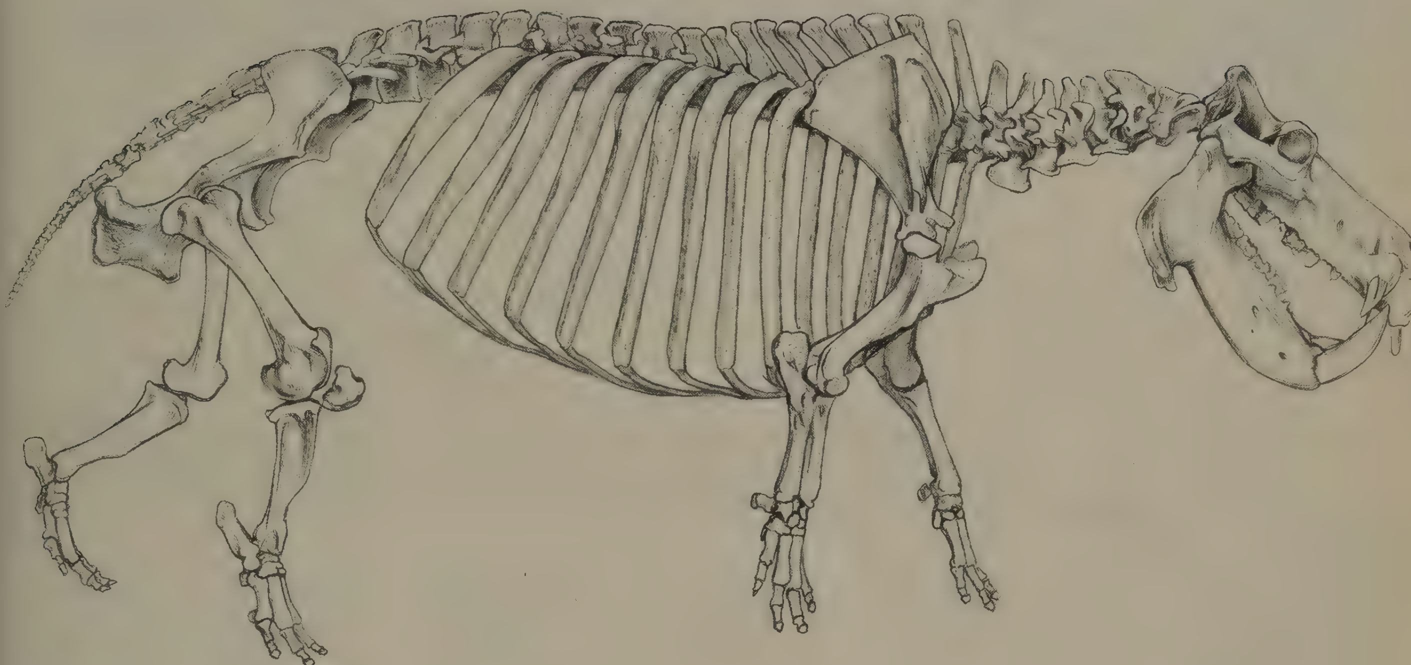
Hippopotamus, Hippo (Hippopotamus amphibius)

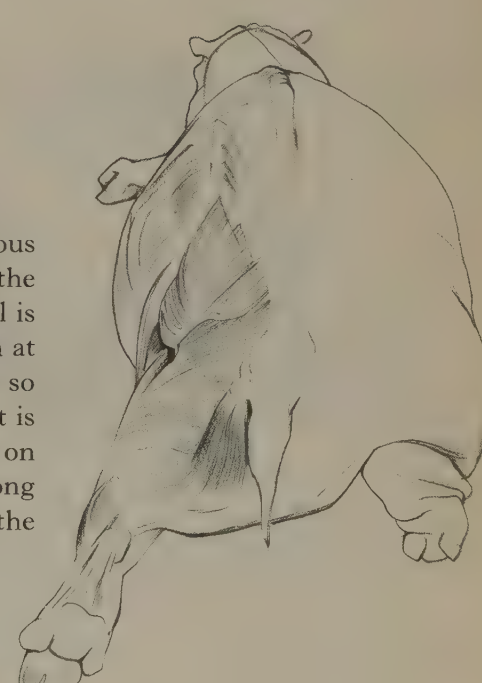
Family Hippopotamidae
Order Artiodactyla
Local names
Kiboko (Kiswahili and many other languages), Kibongho (Kizigua), Ensherre (Runyankole), Eisere (Lukonjo), Tomondo (Kinyaturu), Nsere (Rutoro, Lubwizi), Mbebwa (Kuamba), Enjubu (Lunyoro), Nvubu (Luganda), Ifubhu (Kijita), Ifuru (Luhya), Inguruu (Luragoli), Invuru (Kinyiha), Nguu (Kikamba, Kimeru and Kikuyu), Emiria (Ateso), Magaita (Elkoni), Magawit (Sebei), Kibei (Kalenjin), Iturruka (Kisamburu), Olmakau (Masai), Jir (Somali), Raa, Rawo (Lwo), Arnorbee, Robi (Kiliangulu, Galla), Erobi (Lugbara, Madi).

Measurements
head and body
300—505 cm males
290—430 cm females
height
150—165 cm
tail
40 cm
weight
1,475 (506—3,200) kg males
1,360 (655—2,344) kg females
Average biomass weight 1,000 kg

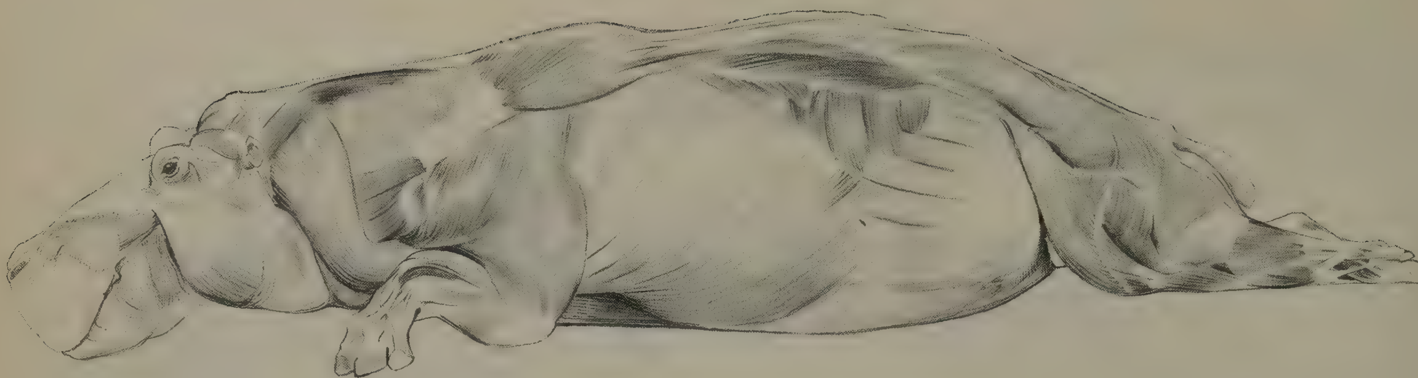
Note : Average measurements are subject to much regional variation

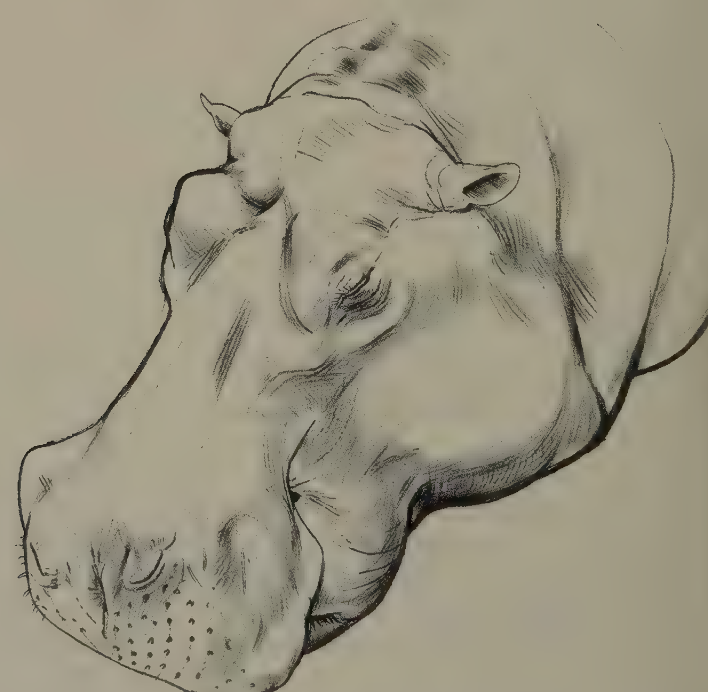
Hippopotamus, Hippo (Hippopotamus amphibius)





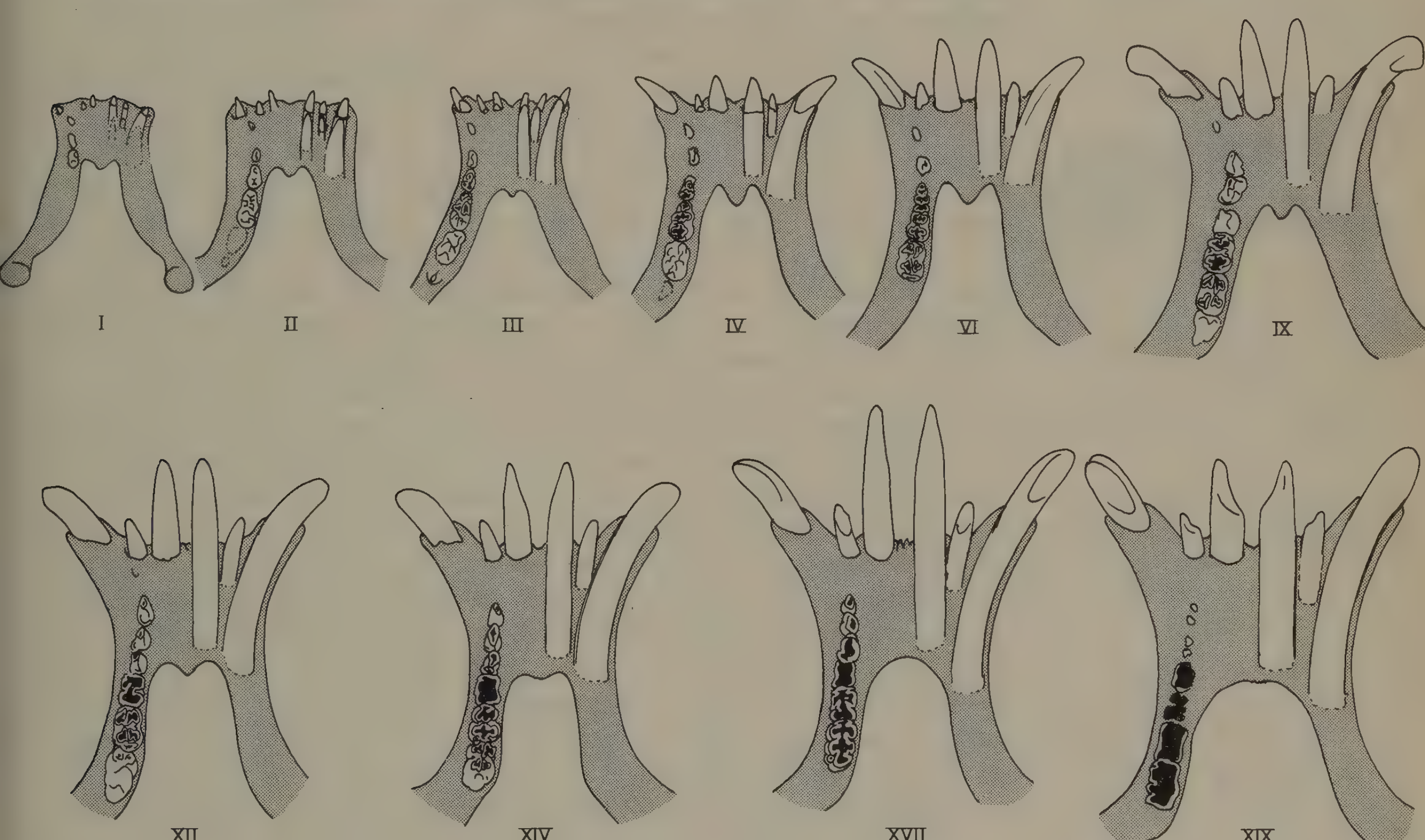
The proportions of the hippopotamus's body reflect its amphibious existence. Its stumpy legs and splayed toes are just adequate to carry the vast, rotund body on land and fold neatly out of the way while the animal is swimming or resting. In spite of their bulk hippos can make a short rush at over 30 km an hour and they are quite adept at climbing very steep banks so long as they have footholds. The size of the limbs is adapted to a life that is largely spent in immobility, lying on their bellies and very occasionally on their backs with feet in the air. Movement in water is assisted by a very long supple back and kicking movements of the hindlimbs, working against the substrate or swimming free off the bottom.





The head is adapted to immersion in that the eyes, ears and nostrils have migrated to the top of the head and the latter are valvular and are opened and closed by small muscles along their margins. The broad, flat-fronted lips are an efficient mechanism to seize and crop grass and the molar teeth, although relatively small, grind up fodder effectively. The canines and incisors, however, play little or no part in feeding and the heavily armoured lower jaw and great baggy jowl are developments entirely linked with ritualized fighting, which determines all relationships in the social life and courtship of the hippopotamus. The jowl is made up of two muscles, a large masseter and an exceptionally well developed digastric muscle, which is attached inside the angle of the lower jaw and loops up behind the masseter to the hyoid. Between them these muscles shut and open the heavily reinforced mandible and the extraordinary development of the angle of the lower jaw is to provide each of these muscles with an enlarged area for their attachment, particularly the digastric, which is capable of opening the lower jaw to an angle of approximately 150°.

The very wide opening of the jaws is necessary because hippos settle contests by clashing their lower jaws together, a practice which leads to a high proportion of males breaking or chipping their teeth. The incisors are modified to act in a manner that is analogous to antler tines in deer, allowing



Dentition and ageing in the hippopotamus (in part after Laws, 1967); Laws age group categories are shown in Roman numerals.

contestants to parry an attacker's onslaught and get a purchase on one another for the pushing that follows the clash: the lower canines serve to take the weight of this activity as well as inflict wounds against rivals or predators.

A peculiarity of the hippo is its short, vertically flattened tail, the vigorous action of which propels the animal's dung out in a centrifugal shower that scatters particles about a metre to either side of the anus. Because of their strictly hierarchical society this ritual is of crucial importance in advertising the status of an individual hippo and all social interactions revolve around the two opposite poles of the body.

The hippopotamus's capacity to remain underwater without coming up for air seems to increase with age. Very young calves submerge for less than half a minute while young hippos range from two minutes to an average adult submergence of four minutes and up to five when alarmed. Sometimes only the nostrils break the surface; alternatively, only nostrils, eyes and ears may protrude and very often the neck is also raised so that the eyes, ears and top of the head are all above the surface of the water—particularly when the water is rough—and the animal has a good look all round. On its surfacing, water is usually expelled from the nostrils with a loud hiss and the very mobile ears are wagged, possibly to empty out the water.

Hearing, smell and sight are quite well developed but the latter sense plays no part in feeding and, in areas where they are persecuted, hippos only emerge from their swampy refuges late on dark nights for a short period of intensive feeding and avoid coming out altogether on bright moonlit nights. In areas where they are reasonably secure from interference and grazing is scarce, feeding may start before dusk or continue into the day.

The hippopotamus's skin is peculiar in being virtually hairless and without sebaceous glands. There are, instead, unique glands which may derive from sweat glands and produce a viscous red fluid. Noting the frequency of wounds, Verheyen (1954) suggested that this secretion might, amongst other functions, provide a healing agent against wounds and this suggestion was tentatively endorsed by Luck and Wright (1964), who considered that the biochemical properties of the secretion were not inconsistent with its being an adaptation to life in contaminated waters. It is possible that it is also a medium for olfactory information about the status of an individual.

The animal's upper surfaces are purplish-grey to blue-black, while the lower surfaces and the skin around the eyes and ears tend to be brownish-pink in colour. Partial albinos have been seen, coloured bright pink with

blotches of liver colour. The endodermis varies considerably in thickness, being five to six centimetres on the back and rump and less than one centimetre thick on parts of the head and belly. By contrast, the outer horny layer of the skin is extremely thin everywhere. Luck and Wright showed that an animal loses great quantities of water through evaporation if it is forced to remain out of the water.

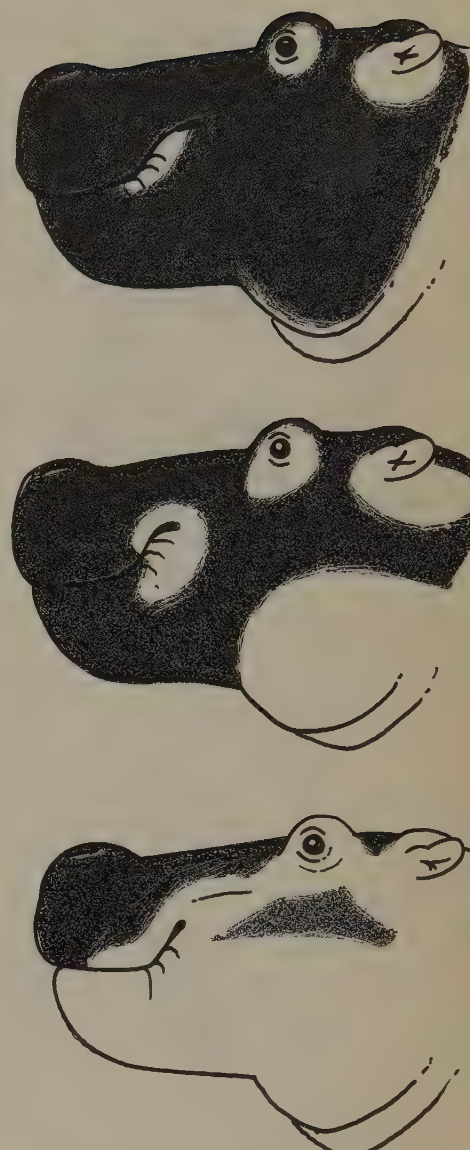
The hippopotamus relies on water or mud to keep cool in hot, dry weather and on sunshine to warm up when the water is cold, which suggests that thermoregulation is not very efficient. In normal circumstances this limitation is unimportant in the well-watered areas of the tropics and subtropics. The hippo may be able to benefit directly from the sun's radiation so long as the compensatory effects of mud and water are available and it probably achieves thereby a considerable saving in metabolic energy. Indeed, a speciality of the hippo might be its strategy for the conservation of energy; several lines of evidence point to this.

Although capable of a fast rush when alarmed or provoked, the hippo has few conspicuously energetic activities. Admittedly, its nightly walk to and from pasture may be quite brisk and confrontations between neighbouring hippos are sometimes far from sluggish but for the rest it spends its time sleeping on sandbanks or lying in the shallows.

In a detailed study of the animal's feeding habits, Field (1970) remarked on the surprisingly small quantities eaten by hippos. His experimental captive weighed about 550 kg and ate an average of 5·4 kg of dry grass per day over a three-month period, without any appreciable loss of condition. Representing about 1% of its body weight, this compares with $2\frac{1}{2}\%$ in cattle and other ruminants. Wild hippos eat only slightly more (up to 1·3%) and few spend more than about five hours grazing; in most habitats they waste no time inland. Females and young suspend all social activity while they graze and get back to the waterside as soon as they have had their fill but I have encountered a male asleep in a bush at about 10·30 p.m. Verheyen (1954) noted a decrease in the range of females with small calves and thought that such individuals could survive many weeks on a diminished food supply.

During several severe droughts around Lakes Rukwa and Katavi it has become clear that hippos can survive in muddy wallows for many weeks without any food, water or shade. Vesey-FitzGerald (1960) suggested they may be living on accumulated fat, which could suffice for the hippo's low metabolic needs in the wallow. This superior endurance represents a positive evolutionary advantage, particularly under fluctuating environmental conditions, as it enables these animals to bypass the worst periods of competition for grazing by simply lying about in pools and wallows. In this way the hippo does not have to compete directly with other ungulates that have superior digestions and feeding techniques and are able to cover greater ranges in search of food.

Thurston *et al.* (1968) have investigated the metabolism of the hippo's stomach. The food is coarsely chewed but is further broken down in the upper three compartments of the stomach, where the action of numerous and diverse species of ciliates assist the carbohydrate fermentation that releases high concentrations of volatile fatty acids. The process of digestion is very much like that of a ruminant and nearly as efficient. However, the



Individual variations in the distribution of pigment on the head.

process must be a relatively slow one, because the stomach holds two days' grass at one time and digestion does not get under way until about midday, many hours after the animal has returned to the water (Field, 1970).

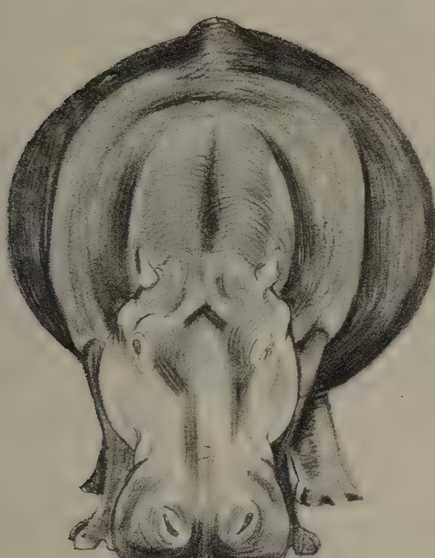
It seems very likely that individuals recognize one another by scent and that the smell of dung may also predetermine the outcome of an interaction, for dung fountains and tail-whirring preceed aggressive jaw clashes as well as relatively friendly encounters. It is possible that for the inferior animal the chances of being attacked by a high-ranking male are reduced after having been scent-marked by him. In this connexion it should be noted that the scent of the male hippo's dung is peculiarly pungent and long-lasting and it may, in certain circumstances, scent the water and mud of a wallow or even a zone of still water surrounding an animal.

While filming hippos in Mzima Springs in 1964, Alan and Joan Root observed that submissive hippos presented wagging tails to a superior with or without an accompaniment of dung. Likewise, a young hippo bottle-reared by Joan Root would respond to puffing expulsions of air by swinging round and wagging its tail, meanwhile peering back over its shoulder (see drawing below). After a brief face-to-face snuffle with its human foster parent, it would usually turn and lean or sit on her foot. Whenever this hippo was excited it yawned.

The males drop their dung at particular landmarks along the hippos' pathways and vast middens as high as the hippo's anus accumulate on the chosen boulder, termitary, stump, root or bush. Males also deliberately defaecate over inferior animals in the shallows.

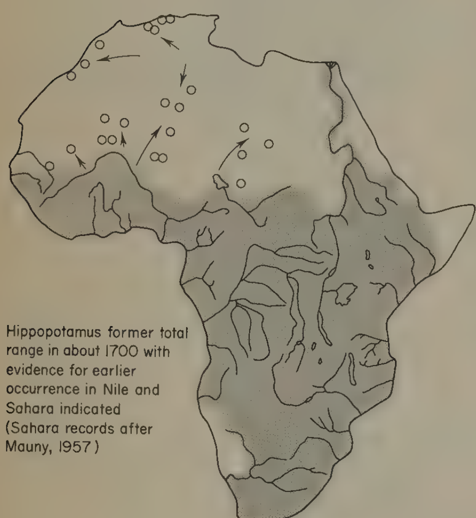
Females, juveniles and some of the small males do not drop their dung conspicuously, nor do they always whirr their tails, but they do pay great attention to the male's dung and juveniles may even lick and eat it. Young animals frequently smell and lick the anal region of other hippos. Apart from that of the dominant males on land, practically all defaecation takes place in the water and this is a factor of some significance in the ecology of lacustrine and riverine habitats in Africa. On the one hand it is a drain on nutriments from the range, but it must be balanced against the immense enrichment of the aquatic environment, which is known to contribute to the extraordinary productivity of the fisheries on Lake George.

Under normal conditions, hippos find themselves grazing the same areas as buffalo, waterbuck, puku, various other antelopes and warthog, which may actually benefit from the grass-pulling and trampling of the hippos (Vesey-FitzGerald, 1960).

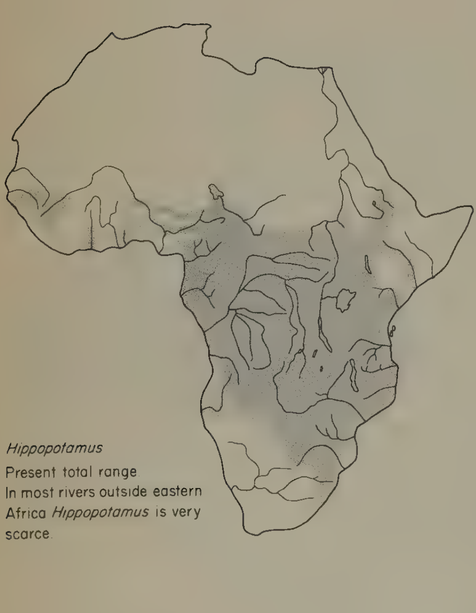


Hippos crop grass entirely by means of their horny lips. They walk slowly and close the lips over a mouthful of grass before the regular swinging of the head wrenches away the grass. The tongue may be used to test the texture and palatability of grass but plays no mechanical role in grazing. The vibrissae of the muzzle may also have tactile value, especially at night. The munching jaws and the heavy breathing of a grazing hippo can be heard at a distance. Weakly rooted grasses are soon eliminated if grazed in this way, while tall tussocks, like those of *Sporobolus*, are more difficult to graze or uproot. The favourite foods of the hippos in the Ruwenzori National Park are *Cynodon dactylon* and *Panicum maximum* (Field, 1970). The former is a

Note opposite page. Hippopotamus distribution is difficult to map because (a) the animals wander very widely in rains; (b) their status changes rapidly; (c) a few individuals often survive in swamps even within densely settled areas; (d) reports seldom suggest relative density. In this map large solid circles indicate the more extensive areas of suitable habitat irrespective of density and include scattered relics of once abundant populations. Elsewhere both relics and smaller populations are indicated by the smaller circles.



Hippopotamus former total range in about 1700 with evidence for earlier occurrence in Nile and Sahara indicated (Sahara records after Mauny, 1957)



Hippopotamus
Present total range
In most rivers outside eastern Africa *Hippopotamus* is very scarce.

creeping species that is highly nutritious, the latter is a tussock grass. A scarcer annual, *Brachiaria decumbens* is a favourite in the rainy season. *Themeda triandra*, *Chloris gayana*, *Setaria* and *Cyperus levigatus* can also be important food species. *Phragmites*, *Typha*, *Pistia*, *Potamogeton* and other water plants are only eaten occasionally, as are the leaves, bark or the fallen fruit of trees, including *Kigelia*, but short grasses are definitely the normal diet in all areas.

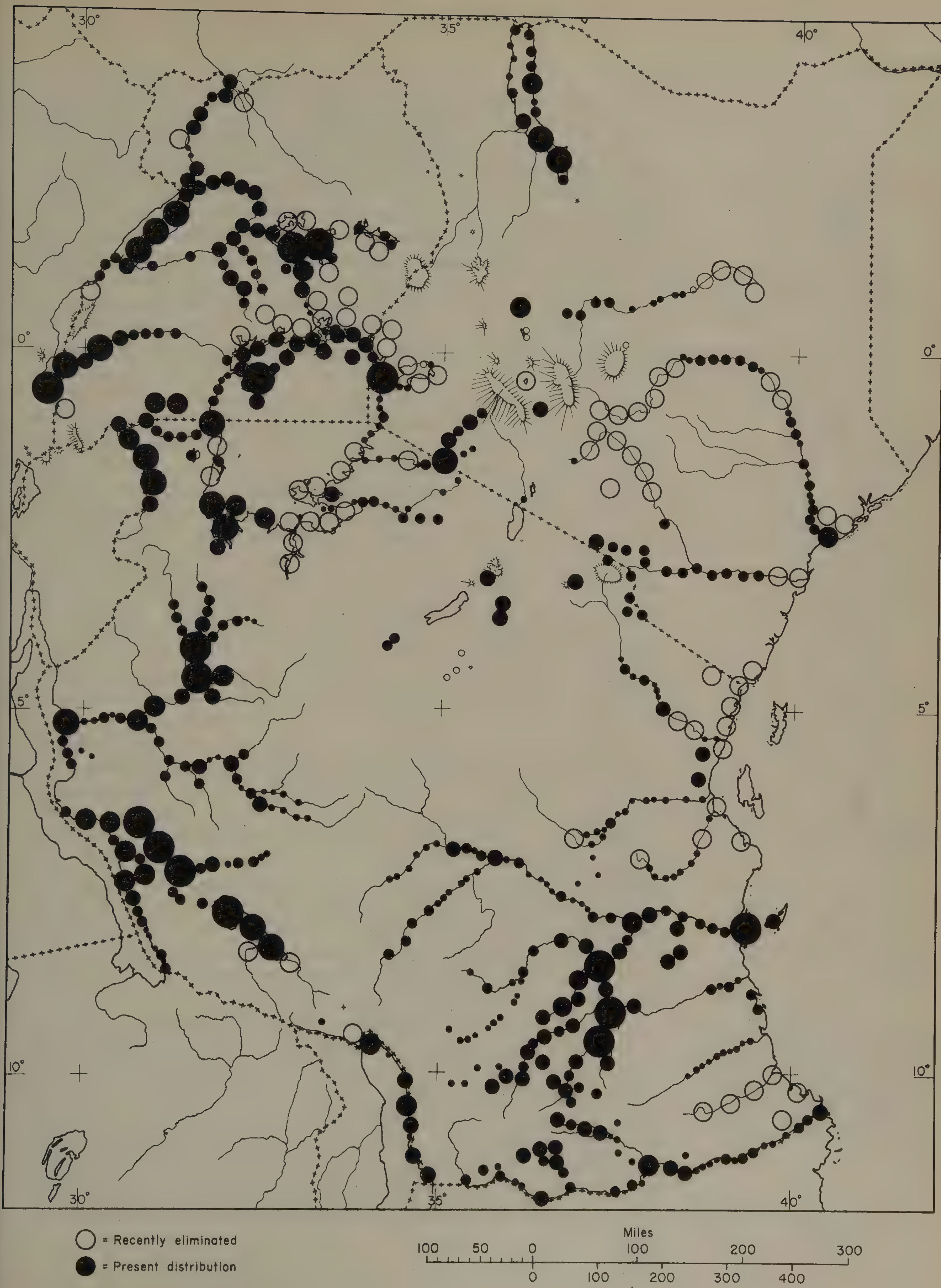
Although fights have been witnessed on land, there do not appear to be any social barriers against individuals ranging freely in search of grazing, but the pasture is reached along well-worn tracks. The furthest a hippo will walk for food is about 10 km with an average of 3 to 5 km, giving the species as a whole a very narrow range around permanent waters. However, during the rains hippos can lie up in temporary ponds or even wet vegetation and so disperse more widely than they do in the dry season and occasionally an individual will wander very widely. The social causes of their dispersion are discussed later but the habit has allowed very remote little lakes and dams in arid country to be colonized as well as the oceanic islands of Mafia and Bijagos. In South Africa, one young female wandered over 1,600 km before being shot. Rainy season visits by single hippos or by small groups have been recorded in many localities where they are not normally resident. Around the vast hippo reservoirs of Lakes George and Edward there is a distinct tendency for hippos to follow rivers up to near their sources in the hills of Kigezi, Toro and Ankole.

It should be noted that wet-season expansions are not associated with a shortage of food. The social system of the hippopotamus reinforces dispersal over the period that the physiological and environmental barriers against it are temporarily lifted.

Their distribution has to be seen in this perspective, for the natural range of the hippo in Africa ran from the Nile delta to the Cape wherever the two requirements of permanent water and open grazing could be met; their upper altitude limit is about 2,000 metres. However, their present distribution is but a fraction of its original range as the hippo's feeding habits do not recommend it to farmers and its meat, fat and ivory are other inducements to hunting.

The nature of the foreshore or the bed of lakes and rivers influence whether they will be used by hippos, as does the depth and flow of the water. A few males can sometimes be found in rocky gorges amidst rapids but the larger groups are generally found where there are relatively firm, gently sloping beaches and quiet waters where each hippo can stand or kneel on the bottom close to the water surface and the young can be suckled without swimming.

The impact of large hippo populations on their environment is very considerable. Because they graze so close to the ground and alter the grass species composition there is no dead grass to catch fire so that small clumps of thicket become a focus for the expansion of dense woody growth. In the Ruwenzori Park, Lock (1967) pointed out that within 3 km of water it was heavy grazing by hippos that excluded fire as the most important influence on the vegetation. Laws *et al.* (1975) correlated the distribution of deciduous thicket along the banks of the Victoria Nile with areas of high hippopotamus



30°
35°
40°
0°
0°
5°
5°
10°
10°
30°
35°
40°
= Recently eliminated
= Present distribution
Miles
100 50 0 100 200 300
0 100 200 300 400
km

density. Major changes in vegetation that are induced by hippos might even deprive them of their pastures in the end.

Dodds and Patton (1968) considered this possibility in attributing the presence of dense mopane thickets around the Lukusuzi River in Zambia to a large hippopotamus population in the past and the regeneration of thicket might in turn have been a decisive factor in their eventual disappearance. Olivier and Laurie (1974) considered evidence for a long-term ecological cycle on the Mara River. They found that the density of trees on one bank was very much greater than on the other, so it was used less by the hippos although the regeneration might have been the product of intensive use by hippos in the past. The possibilities for a long-term cycling of hippopotamus populations in relation to their habitat are obvious but since men and elephants frequently share these habitats they too would commonly enter into the ecological equation.

There are generally a number of adult males within an aggregation of hippos but there are also many solitary peripheral males that generally rest in less favoured localities, and in a dense population some of these may lie up in mere puddles or in long grass, possibly because their return to the water is blocked by larger males. Indeed the dung deposits made by dominant males along the foreshore and on exit paths might be a deterrent to inferior animals attempting to re-enter the water. Almost all dung deposits on dry land are made by adult males and when disturbed they often emerge from the water during the day to augment deposits on the foreshore. From what is known about mammalian marking procedures in general, it seems likely that the deposit becomes a sign that not only helps the male familiarize himself with his home range but also informs other hippos of a male's presence. The reaction of another hippo must then depend on its individual status and experience.

Hediger (1951) saw these deposits as evidence for terrestrial territories and mistakenly imagined that the hippo paths radiating from the water defined the pear-shaped territory boundaries. Verheyen (1954) described hippo society as a hierarchical matriarchy but did not recognize individual males or record their movements. He saw very frequent contests as evidence of males' territories in the water instead of on land. The matriarchal elements observed by Verheyen may turn out to be a direct response to peculiarly high density (see below). During a two-month study in the Serengeti Park, Olivier and Laurie (1974) confirmed a dominance hierarchy including males and females but recognizable individuals could be seen at widely different places on the river during this time. These authors did not therefore consider that hippos have any territories in the water or on land.

A long-term study of the social life of the hippopotamus is in progress in Ruwenzori National Park, where Hans Klingel has determined that the males occupy mating territories in a narrow strip of water and land along the foreshore, the exact size of which seems to be quite variable. He has found that the schools simulate a certain cohesiveness because the individuals are resident in a particular area but these are unstable associations of all classes except for mothers with their young which can stay together for several years. Bachelor males form groups but these are also unstable in composition and like all hippo groups subject to considerable variation in numbers. At night

Distribution of hippopotamus groups along a stretch of the Nile (near Chobe) (after Laws *et al.*, 1975). Note solitary animals (nearly always males) scattered down both banks and large herds' preference for shallows near the mouths of tributaries.

only mothers with young keep close together and animals graze as solitary individuals in spite of several hippos being close to each other for a considerable time (Klingel, personal communication).

No long-term study of hippopotamus behaviour has been completed yet. Most of their social life occurs in the water where much of what happens is out of sight and the recognition of sexes, let alone individuals, is difficult. However, immobilization and ear marking should be feasible and the social implications of the hippo's seasonal breeding peaks are one of several promising subjects for future study. It would also be interesting to learn how the sexes and different classes are dispersed as the seasons change and to have more detailed information on the fundamental differences between small isolated populations or groups and the huge concentrations of western Uganda.

Male hippos defend their immediate vicinity but the size and location of this area and the degree of their intolerance may alter with local conditions and with the seasons. Their behaviour is possibly also influenced by female sexual cycles. In certain circumstances males are aggressive towards most other classes including females and particularly very small young. Adult male hippos can be possessive about exit–entry paths between water and grazing and I have seen a spectacular fight on the foreshore at such a point in the early morning. At other times they fight in the water as a result of trying to control the movements of females while on other occasions fights erupt in open water or on the grazing grounds.

The basic social unit is the mother and her young and it is not uncommon to see a female closely followed by a file of up to four smaller animals, graded in size from a tiny infant to a three-quarter-grown young one. It is not known if these are necessarily her own offspring, for females apparently tolerate unrelated young and subadult animals, but the attachment of a baby to its mother is very marked and she is the focus for all activity. These units are most readily recognized while the animals are grazing, but can sometimes be discerned when larger groups are scattered through a stretch of open water.

For the female and young, most social life takes place in the water or at the water's edge. All dangers are met by the mother and she is exceptionally aggressive and willing to protect her young from predators; during any alarm her young tend to cluster very close to her. Scattered groups in the water can also be seen to draw together when disturbed. Furthermore, there is a distinct tendency for hippos to aggregate into larger groups in response to danger, which may derive from this infantile habit. Verheyen (1954) stressed that the young are introduced to aggression from the very beginning. He saw mother hippos nudge, swipe or even bite at their young if they got out of line or started playing or wandering while walking to pasture. At this time the hippos often trudge along in a rank order, each animal patiently waiting for the one ahead to move and the maintenance of paths may be due to the tendency for inferiors to follow seniors in line.

Within a family unit the youngest animals are closest to the female. The juvenile prostrates itself whenever it is threatened by the mother and this gesture is carried over into adult life as the principal appeasing gesture. The mother often licks, nuzzles and scrapes her offspring with her lower incisors

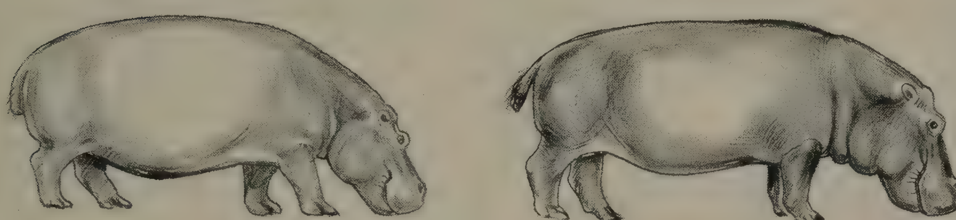
and even adults will groom another full-grown animal, particularly when the partner is lying prostrate. The behaviour appears to have a reassuring function and it is sometimes followed by the groomer's resting its head on the other animal's back, which is also a common expression of sociability. Nonetheless, it is not unusual for quite small hippos to have severe cuts, evidence of an early introduction to an aggressive society.

The nightly scatter over the grazing grounds and seasonal dispersal of entire populations discourage sustained ties between adults and there is no evidence that they occur. A male's interest in mating must also be of limited duration and he is unlikely to be able to control more than one female at a time. Any structuring of social groups above that of a mother and her young is therefore likely to be of a rather temporary nature. Attwell (1963) thought that large herds were merely an indication of crowding brought about by lack of suitable reaches of water, whereas small schools indicated better conditions. While this probably applies at the broadest level of generalization, there is also evidence that different classes interact in such a way as to bring about recognizably distinct social structures, even if only for brief periods. For example, small mixed schools often seem to be made up of several males shepherding females. Physick (1972) described a male turning back a female that attempted to leave his group for another, 500 metres away. This male was immediately challenged by a male from the other group and as soon as he approached it a clash ensued.

While males may induce a ward-like type of social cohesion when they are sexually interested in females, their aggressiveness might also be the primary reason for a type of aggregation which Verheyen (1954) termed a nursery herd. Nurseries might be formed as a result of the natural defensive bunching of young round a female and, by extension, of female unit to female unit. Verheyen saw incidents which suggested that a female's readiness to defend the young may also extend to other females and he suggested that female cooperation directed against adult males could ensure that nurseries occupy the best, most graduated beaches. Individual mothers have been seen to leave such aggregations, their young remaining with the rest of the group. This desertion would seem to contradict Verheyen's hypothesis; Babault (1949) saw one such herd in which 40 very young hippos had been left with only one adult. But if mating involves danger for the young, nurseries could actually favour the young in more than one way, by allowing oestrous females to desert their young temporarily while being mated. Both the existence of nurseries and the killing of very small hippos by large males may be traits that are exaggerated in dense populations and by the temporary concentration of animals during the dry season. The Lake Edward population was already of exceptional density when Phillips (1929) recorded large numbers of infant hippos killed by adults, and the phenomenon has been widely reported since. Verheyen actually catagorized the adult male as the major enemy of young hippos in the Upper Ituri. He pointed out that even young females reared in captivity are very protective of their newborn against the male and he posed the question of motive when the male licks a newborn baby on land but attacks it in the water. He suggested that a male is sexually attracted exclusively to the mother, remaining fiercely intolerant of any other intruder into his own water. Verheyen noted that in the relative absence of

natural predators the overall effect of the male's behaviour is to reduce density.

Laws (1967) recorded an increase in the proportion of calves in the Ruwenzori Park population after some 3,000 hippos had been shot. Although the shooting had tended to select older and larger animals and thus bias the ratio in favour of the young, there was a rise in the proportion of calves less than one year old from 5% in 1958 to 14% in 1965. It is possible that this dramatic increase in the ratio of small young could have been assisted by the removal of some of the big males as their principal predators. Laws (1965) considered that calf mortality had a relationship with group size but the increase was assumed, however, to be due to an increased calving rate in the females.



Sexual dimorphism. Note the massive development of the forequarters and jowl in the male (left).

One of the reasons female groups are able to repel a larger, heavier male might be that the latter's method of fighting is more ritualized, whereas females are more prone to use their teeth for directed bites rather than parry a series of jaw clashes. They also tend to break the rules by launching concerted attacks and coming in from the side.

Although all classes of hippopotamus fight, the tendency is most marked in males and this from an early age. Evenly matched youngsters repeatedly test one another's willingness to fight with jaw displays and clashes. In an uneven match a male has two options when he is challenged by a larger animal; the commonest reaction is to flee, but alternatively he may appease his superior by prostration. The latter course has the advantage that it allows it to continue its existence in the immediate vicinity of a large male but is linked with perpetually obsequious behaviour. When a challenge comes from a male of the same size, it is more likely to be taken up and this could be the explanation for a high incidence of fighting in overpopulated areas. Exclusion by the older and heavier males forces inferior males into peripheral areas (see map). In this connexion it is interesting to see how the odds are stacked in favour of the oldest males because they continue to grow, albeit very slowly, throughout life, whereas females stabilize (see Laws, 1968). Although size is probably a major determinant in male contests, individual disposition is also important. Verheyen (1954) described seeing a large, full-sized male that was entirely free from scars and this animal consistently refused to fight, even when the challenge came from a smaller but more aggressive animal.

The jaw display is essentially a visual advertisement of willingness to fight. The head rears out of the water exposing pale cheeks and chest and a brilliant pink gape as the mouth snaps open. This is further advertised by a

reverberating nasal wheeze followed by a series of guttural honks. This call is uttered in the early mornings and may be associated with the animals taking up stations in the water after grazing. It is the invariable response to disturbances of the *status quo*, particularly in the evenings, when individuals start to move about and prepare to leave the water. Wheeze-honking tends to lack directness and has been provoked by playing back a recording. Nonetheless, it is often uttered as two animals approach one another, and the loud wheezing bellow or roar that is made while they actually clash jaws may be simply an abbreviated, more intense repetition of this call. If two males confront one another, they raise their rumps above the surface of the water and whirr a fountain of dung; then with immense yawns they ram their open jaws together in a heavy clash. Verheyen (1954) thought that the angle of the yawn increases with age and he noted that the red glandular secretion becomes very copious in fighting males and in females about to give birth—giving their eyes and faces the appearance of being covered in blood. If one contestant loses ground in the pushing and jaw clashing that follows, it may adopt a submissive posture but it is more likely to break away and, whipping round, present only its retreating rump to the victor.

The skin of the back, rump and sides is up to 6 cm thick and no such thickening is found at the front end of the animal, which conforms with the observation that contestants normally succeed in parrying every advance with a clash of teeth. Occasionally a yawn display may be preceded by a forward scooping up of water, weeds and *Pistia* in the mouth, which is emptied in a violent sideways toss. In densely packed groups the first sign of a jaw clashing match may be a rearing sideways toss of the head and a clash may also end with a few desultory tosses. These clashes are distinct from all-out fighting and among the younger hippos they give the impression of being an activity that is sought out. It is drawn out into a ritual lasting an hour or more with periods during which the open jaws rest chin to chin and muzzle to muzzle with no attempt at biting but there is occasionally straining so that both jaws may be forced further open. Sparring partners stimulate other males, particularly those in the immediate vicinity and it is not uncommon to see males that are quite distant but within earshot rouse themselves and reply with wheeze-honking, dung fountains or yawning when they hear the clash of teeth or a wheezing roar. Onlookers to a jaw-clashing match may toss their heads or yawn. If another animal is touched during a match it may attack one contestant, which may then be forced to spar with him. On such occasions I have seen the former sparring partner plunge under the surface, come up between the two other animals, and displace the interrupter with his backside and thus resume the contest. However, the clashes are usually strictly head-on and only between two contestants.

From scattered observations of hippopotamus populations across Africa it would seem that both group sizes and social behaviour may be significantly affected by density. Where populations are large the density of individuals seems likely to intensify male contacts and competition and makes it more likely that strangers may meet.

The grasslands surrounding Lakes Edward and George support the largest population of hippos anywhere in Africa. After a detailed survey of

the Uganda Park sector, Laws (1965) found that the average grazing density was 17·4 per sq. km and in some areas numbers reached 31 per sq. km.

Overgrazing was first recorded in 1937 but began to cause anxiety soon after the inauguration of this area as a national park and Bere (1959) described the initiation of a controlled cropping scheme which has been maintained since that time. This has aimed to stabilize densities at an estimated optimum of about 8 per sq. km. Officially controlled cropping started as early as 1933 on the Rufiji River in Tanganyika, at which time 2,600 animals were killed. There was a decline in the average weight of teeth from over 3 kg to about 2 kg, implying changes in the age structure of the population, which accords with the experience of Laws (1968) in the Ruwenzori Park.

In most lake and riverside areas hippos have been eliminated or dramatically reduced as the land has been progressively colonized by farmers. Between 1950–54, 12,500 kg of hippo tusks were officially recorded and exported from the West Nile area. This would have represented about 3,000 animals.

Hippopotami have always played a very important part in the lives of the river and likeside people. In the Niger delta large hippopotamus masks worn on top of the head featured in the important Owu water festival. In ancient Egypt the hippo was associated with a female deity of pregnancy and was often represented in tomb murals as being harpooned from boats; they were also the victims of the Roman circuses.

Because their movements are relatively easy to control, it is conceivable that hippos could be managed in many areas outside national parks on a sustained yield basis, possibly in conjunction with other livestock. If fish were kept in their ponds they might prove to be a useful adjunct to pisciculture. Controlled management has not been attempted yet, although hippos have proved extremely hardy and breed well in captivity. They tame reasonably well and have lived up to 50 years in zoos.

In terms of grass consumption, hippos are, as was mentioned earlier, exceptionally economical for their size and, in moderate densities, they probably improve the pasture for other animals. Their potential for cropping is proven but the usual logistic problems are intensified with the speed with which a carcass perishes in hot weather. The meat is very palatable and makes good hams. The popularity of hippopotamus meat has probably been the main reason for many hundreds of hippos being shot every year on "control". Hippos are, in fact, easy to control by means of ditches or small fences and are even deterred by low wire, particularly if it is hung with rattling tins (Clarke, 1953).

Hippos sometimes upset small boats but rarely attack people on dry land unless provoked. Their charge is fast; the back appears to be hunched, the head is carried low and shakes from side to side as the jaws champ up and down and the animal seems to froth at the mouth.

An unusual observation by a party of visitors in the Ruwenzori Park concerned a hippopotamus they were following on land, which charged up to two lions concealed near the vehicle and with partially open mouth "aimed some spittle at them". Remembering the submissive behaviour of a captive in response to puffing, this behaviour might betray some curious form of intraspecific threat.

The hippo's defensive reactions vary. A harassed one on land tries to make for the water but, if hard pressed, it either charges or gets its backside into a bush and threatens with its jaws. Young hippos often escape from adult males by scrambling ashore, and in areas where they are commonly harpooned from boats they also flee the river and make for dense cover on land or in the swamps. Likewise, wounded individuals have been reported to lie up out of the water while their wounds recover.

Females have been recorded killing lions in defence of their young and there are odd records of apparently unprovoked attacks on tied-up goats, watering rhinos, a wading elephant and people. In contrast, hippos have occasionally been seen to nibble at the wallowing buffaloes that share the shallows with them, behaviour which could be explained as misdirected grooming elicited by the buffaloes' prostrate hippo-like form. Similar inter-specific grooming sequences have been seen in Rotterdam Zoo by Van Doom, where a male living with an aged female took to standing on the trench rim that separated him from some elephants and shook his open-mouthed head at them:

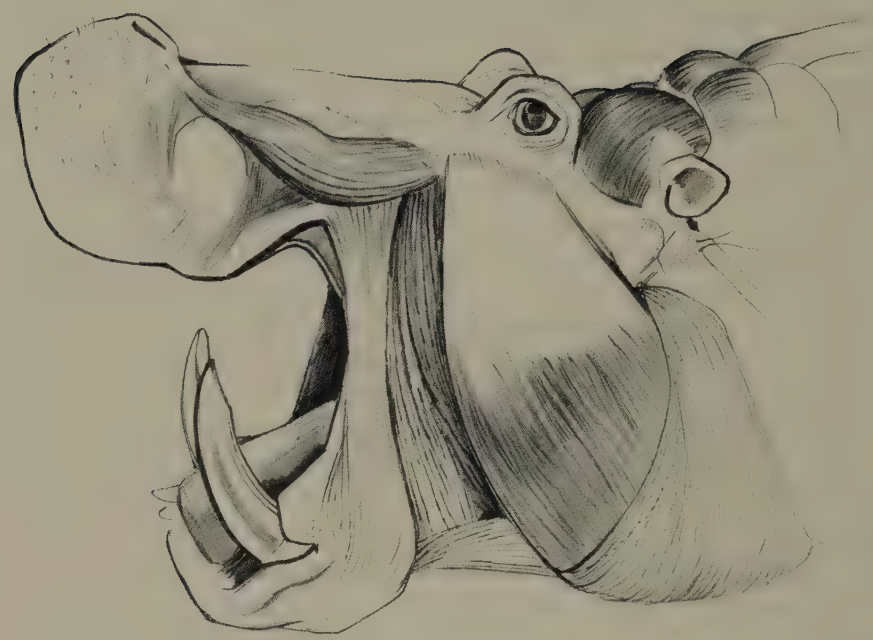
> "the elephants put their trunks into the hippo's open mouth or they rubbed their tusks on the hippo's canines or they allowed him to gently nibble at their foreheads and the bases of their trunks. Some of the animals offered a hindleg, an ear or even a tail. The hippo grasped these parts very carefully with his jaws without actually biting" (in Grzimek, 1972).

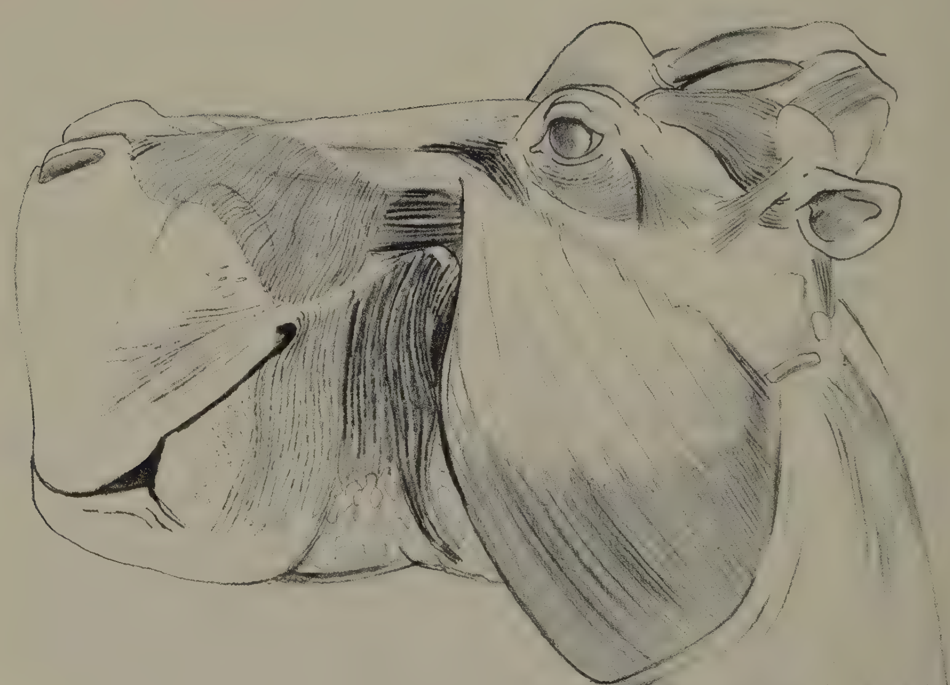
The only serious predators of the hippopotamus are hyaenas and lions. Both species take calves but lions occasionally attempt to kill adults, a task they generally find very difficult and on one occasion lions were found feeding on the living animal after nearly killing it. However, killing a hippo may be a matter of technique, for Guggisberg (1961) described lions killing two fully grown hippos by rolling them on their backs and biting the chest and throat. A very unusual incident occurred in the Ruwenzori Park when a hippopotamus was gored to death among a herd of buffaloes and there are other records of hippos being killed by elephants.

The hippo's unusual hardiness has already been mentioned, but drought and starvation take a heavy toll when prolonged for several months, as happened in 1948 when the northern lagoon of Lake Rukwa dried out completely.

In general, hippos appear to suffer less from disease than most ungulates but there have been reports of deaths from anthrax. This disease is contracted by both ungulates and carnivores and the hippo is exposed to it because the chief source of infection is watering places. It is possible that this disease was responsible for an undiagnosed epizootic which killed many hippos in 1937 around Lakes George and Edward. Although there was considerable mortality, the disease seemed to be of short duration. Laws (1968) found antibodies for rinderpest in the blood of Uganda hippos aged about twenty or more and although there is no evidence that the disease is fatal it is known that the Ruwenzori Park population was exposed to rinderpest in 1929, in 1932–33 and in 1944–46. Parasites include stomach and liver flukes, intestinal worms and protozoa. They also attract leeches and ticks.

Hippos are seasonal breeders. In Uganda calves are born mostly during two periods of the year, October and April, when they might benefit in some





unknown way from being born during the rains. There is a correlation between mating peaks and dry spells, at which time the hippopotamus population is most concentrated. The timing is due to the females' being seasonally polyoestrous, whereas the males show no evidence of sexual fluctuations (Laws and Clough, 1965, 1966).

In this very aggressive species, it is interesting that the male forces the female into a state of complete submission in order to achieve copulation. Verheyen (1954) has contrasted this with the very discreet demeanour of a large male circulating among females, possibly testing for signs of an oestrous one. If a female stands up or there is an alarm, he lies down, stopping to dispense a shower of dung over the densely packed nursery herd. He moves very slowly among its members and shows no trace of aggression. Once he has found an oestrous female he pursues her until she turns round and clashes jaws. The pushing contest that follows takes place in the shallows and the male's superior size and weight are decisive, and the female finally adopts the prostrate position which allows the male to mount. As she is generally submerged, she has to raise her head to breathe occasionally and even though he is copulating the male snaps whenever her head breaks the surface, thus reinforcing his dominance and her submission.

The female is often scratched by the male's hooves and she may make several attempts to break away before she succeeds and once again joins her young or female group. The male's courtship is often punctuated by wheeze-honking. Verheyen (1951) asserted that oestrous females answer his call but Scotcher (1973a) only heard the male call during courtship.

The gestation period is about 240 days and the female becomes very aggressive shortly before giving birth. The birth takes place on land or in the shallows. Bere (1959) reported that there were points that were regularly visited by females to drop their young and suckle them. Senior and Tong (1963) and Kirchshofer (1970) have given detailed accounts of parturition in zoos.

Newly born hippos are relatively small but can vary in weight from 25·4 to 55 kg. Brooks (1961) shot a female containing monozygous twins but this is a rare occurrence and Laws and Clough (1965) found only two sets of twins in nearly 300 pregnancies. These authors defined the average female cycle as eight months gestation, twelve months lactation and four

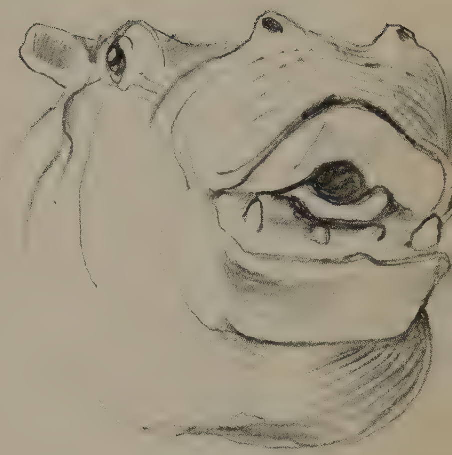
month's anoestrus but they did find evidence of a post-partum oestrus and noted that 10% of lactating females were pregnant.

Suckling takes place on land or in the water but the young show sucking behaviour that is adapted to submersion irrespective of the animals' situation and which can be seen when they are sucking from a bottle, at which time the tongue rather than the horny lips hold the teat (see drawing). The young one interrupts drinking to gasp, then breathes deeply before continuing with closed nostrils and folded ears.

Lactation lasts for about a year but the young hippopotamus starts to chew grass at about one month and to graze at five months.

Young hippos are sociable and play with their age-mates, indulging in chases and mock jaw clashes. As was mentioned earlier, it is probably during this period that hippos learn to take one another's measure. Mutual licking and grooming between mother and calf are common. Laws and Clough (1965) determined that the sex ratio is equal. Zoo-bred females have matured at less than five years and males rather earlier but females in the Ruwenzori Park are sexually mature at about nine (seven to fifteen years), while males become sexually active between four and eleven years of age.

Laws (1968) has elaborated an age grouping technique by using lower jaws and by referring to known-aged jaws he arrived at absolute age grades, culminating in natural death at forty to fifty years.



Young hippo sucking with open mouth using flat fronted tongue against roof of mouth.

Camels

Camel striding

TYLOPODA
Camelidae

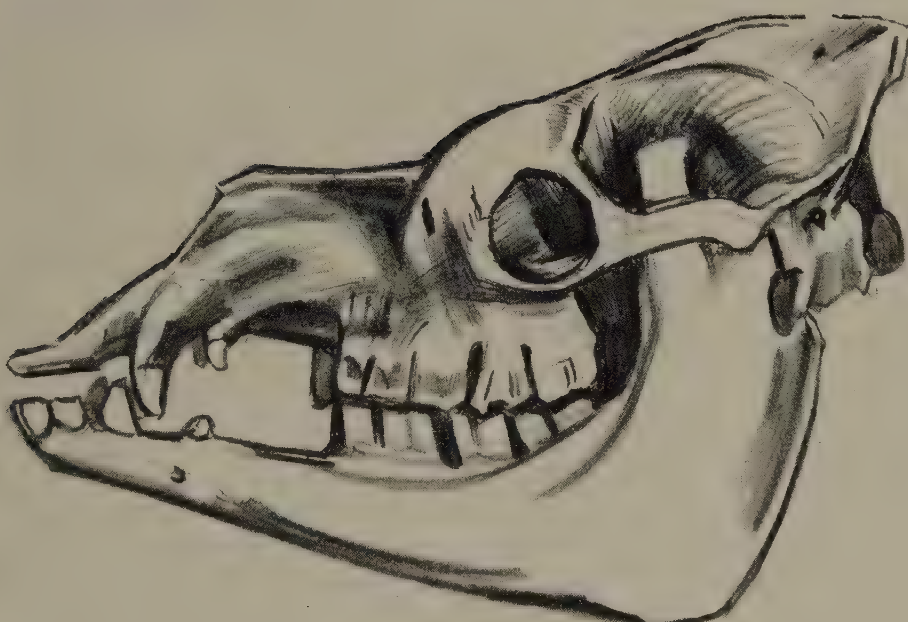
The tylopods originated from an early swine-like artiodactyl and the groups radiated during the Eocene into several distinct families.

In many Oligocene deposits of North America and Eurasia, tylopods are dominant mammals but their name, which means "cushion foot" and derives from a peculiarity of the modern camels, is misleading because these early members of a very varied lineage included short-legged and hoofed animals with feet and figures quite unlike those of camels.

The Camelidae or true camels can be identified in *Poebrodon* of the Upper Eocene and in *Poebrotherium* and *Dyseotylopus* of the Eocene. Like the horses, camelids originated in North America and they evolved long unguligrade limbs earlier than any other artiodactyl lineage (see p. 183). Among the various American Miocene camels were tall giraffe-like animals and a slender gazelle-like form.

The modern camels' lineage includes the Miocene *Procamelus* and a variety of camels known from the Pleistocene in America and Russia. The earliest fossils from Africa are from the late Pliocene of Omo (Howell *et al.*, 1969) and the mid-Pleistocene of Olduvai implying rather dry open habitats at those times.

Some of the characteristics of camels are described in the following profile.



Camel, Dromedary (Camelus dromedarius)

Family	Camelidae
Order	Artiodactyla

Measurements
head and body
2·5—3·0 m
height
1·7—2·3 m
tail
35—55 cm
weight
300—500 kg
Average biomass weight
304 kg

Camel, Dromedary (Camelus dromedarius)

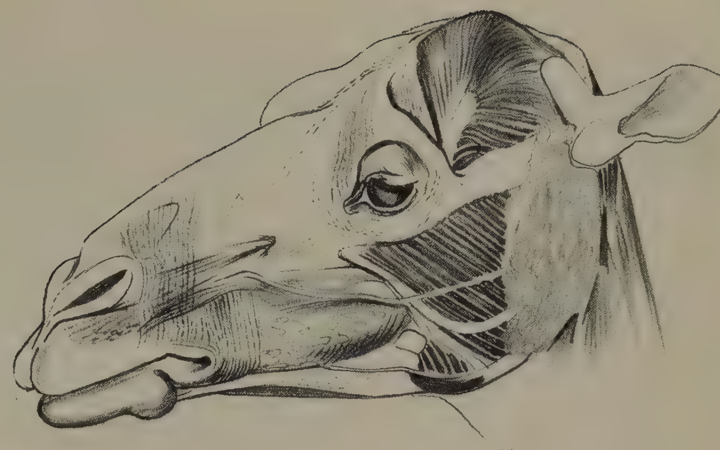
The name "camel" derives directly from the Arabic *gimel* and this animal's association with the Arab world is a very ancient and persistent one. In fact, it was probably in Arabia that the dromedary was first domesticated, perhaps as long ago as 4000 B.C. Today dromedaries are only found under domestication or in a feral state but *Camelus* existed in eastern Africa in the middle of the Pleistocene and as early as three million years ago; fossil remains have been found on the Marsabit road, at Olduvai and Omo (Howell *et al.*, 1969). These Pleistocene camels probably differed very little from the living form but the two Omo specimens are certainly from a larger animal and Gentry and Gentry (1970) suggest that an Olduvai specimen might represent *Camelus thomasi*, a species that is better known from Eurasian deposits.

In spite of being an important domestic animal in all desert regions of Africa and Asia many of the camel's unique adaptations to desert life have only been investigated in recent years and its physiology has been revealed as an extraordinarily refined system of great interest.

The loose and sandy soils of the desert present problems which the camel's feet are well designed to cope with. The peculiar toes splay as they touch the ground and the cushion beneath them squelches out as the weight of the animal bears down. In this way a broad flat plate of elastic material encounters the soil and gives a firm base for levering the body over a ground surface which does not allow feet any purchase for a kick-off. Exceptional rotation at the first digital joint avoids disturbing the footpad (a consideration that can be appreciated by anyone who has hiked over sand dunes). Flexibility at the fetlock is particularly crucial for another reason; the camel's pacing gait requires the weight-bearing limbs on one side of the body to pivot simultaneously in the same plane, while the two limbs on the other side of the body swing forward together in a long synchronized stride. Pacing thus allows this long-legged animal to manage a difficult environment with economy, both in the number of steps it takes over a given distance and in the energy it expends in doing so. The area of the forepads is larger than that of the rear pads because more than 65% of the camel's weight is carried down the axis of the exceptionally long shoulders, which flank a deep but very narrow chest. Extending forward from the shoulders, the long heavily boned neck is suspended by a particularly powerful nuchal ligament, which is a continuous tension member between head and sacrum pivoting on the withers. This concentration of weight and balance in the shoulder is responsible for the very peculiar profile of a camel with its high constricted waist sloping steeply down into the low-slung chest and the thin, straight hindlegs. The advantage of this arrangement is that balance is easily shifted so that it lies directly above the foreleg that is bearing the weight. The side-to-side swaying of a pacing camel is minimized by the narrowness of the chest and there is an economy of effort, because relatively small contractions of the *trapezius* and *deltoid* will pull the body's centre of gravity over to whichever side the feet are planted on. Dagg (1974) and Webb (1972) have investigated camel gaits

and the former has observed significant differences between fast and slow pacing and between young and old camels.

The muscles of the neck are particularly well developed, so that the balancing function of this organ is well served. However, the neck is also the camel's principal weapon in ritual fighting and it is astonishing to see how effectively the lower surface can be used to force down another camel's neck or, as a coiled ram, to unbalance the opponent. The exceptional size of the vertebrae has probably been adapted to these uses of the neck.



A camel is sharp-sighted and has an acute sense of smell. The eyes are protected by dense tufts of vibrissae above and below the eyes which supplement the eyelashes. The nostrils are valvular and, when almost closed, the surrounding hairs are probably able to exclude fine sand while the animal can still breathe, which would be useful in sand storms.

The camel's hump, which is a deposit of fat, probably has more than one function. Together with the woolly coat it must insulate the body to some extent from the heat of the sun. As the animal has a variable body temperature, which sometimes drops as low as 34°C during the night, the slow conduction of heat through fat probably allows the hump to delay the impact of the sun's radiation on deeper parts of the body. When camels huddle together on a very hot day their humps may be acting as heat umbrellas. The fat is also a source of stored energy. Water is not stored in the hump, as is often asserted, but it has been suggested that the hydrogen molecules of the fat might combine with free oxygen to produce metabolic water. Water is conserved by the camel better than by any other large mammal and it has several strategies to manage on minimal water, which have been investigated and described by Schmit–Nielsen *et al.* (1956, 1957). In the first place a camel does not have many sweat glands and can allow the body temperature to rise to 40°C before it sweats. By this means water is conserved which would be lost otherwise through evaporation. This heat is dissipated during the cool night. The camel avoids wasting water by concentrating the urine and transferring urea to the stomach, where microfauna and flora convert it into usable amino acids. In the three-chambered stomach and foregut the camel has a very peculiar water circulation system by which moisture is absorbed into the blood, perhaps by osmosis, and recirculated back into the stomach through copious amounts of saliva. Hoppe *et al.* (1974) inserted a tube into the salivary

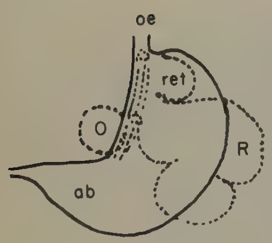
glands of the camel and found that one parotid gland produced as much as 15 litres a day. It is probably this concentration of liquid in parts of the stomach that gave rise to the legend of camels storing water in their stomachs.

These adaptations appear to be linked with a peculiarly efficient circulation of the blood, the corpuscles of which have a remarkable elasticity. Under the effects of heat stress and water loss, the camel shows no ill effects as its body becomes progressively dehydrated. A camel can lose over 30% of its body weight through desiccation but the blood continues to circulate efficiently because the plasma maintains its original viscosity. When a camel has become dehydrated and then suddenly has access to water it is capable of drinking up to 135 litres of water in thirteen minutes. The rapid inflow of water swells the resilient blood corpuscles to as much as 240% of their original volume without bursting. However, if they do burst, the membrane of the corpuscle simply reverts to its original size and oval shape (Peck, 1939). Young camels have blood cells even more resistant to the effects of rapid large-scale drinking.

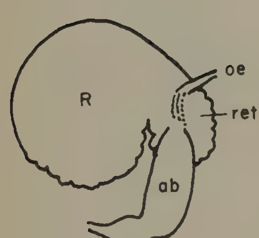
The structure and colour of the wool encourage the reflection of heat and good insulation delays the build-up of temperatures over 40°C, so that before the body has become too hot, the accumulated heat can start to dissipate in the cool of the evening and night. Normally the animals rest in the heat of the day and in the desert's hot season they lie in tightly wedged huddles, occasionally shuffling their positions so that they remain facing the sun, thus exposing a minimal surface to radiation.

In addition to this extraordinary range of capabilities, camels are able, under some circumstances, to drink water that is more salty than the sea (Maloiy, 1972a). The physiology of this animal is the subject of intensive research at Nairobi University, where Dr Maloiy is preparing a monograph on the dromedary.

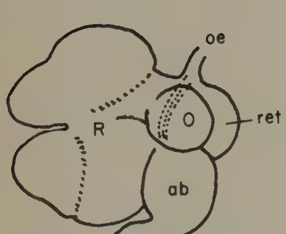
Camels have been recorded eating about 200 species of plants (Gauthier–Pilters, 1974). In many desert areas the dominant grasses are species of *Aristida* and *Panicum* and these are vitally important foods for the camel. In Kenya, Sato (1977) has recorded Rendille camels taking 45·7% of their food from trees and shrubs, 25·5% herbs and vines and 28·8% grasses. The major food species were *Blepharis linariifolia*, *Duosperma eremophilum*, *Sericocomopsis pallida*, *Indigofera spinosa* and *Tephrosia uniflora*. *Acacia nubica*, *A. paolii*, *A. reficiens* and *A. tortilis* were recorded from the Laisamis area. At times they feed to a large extent on acacias, using the independently mobile upper lip and tongue to draw the thorny branches and leaves into the mouth, where they are seized and cut against the sharp lower incisors. In spite of taking small bites and moving continuously, camels remain healthy on as little as 5 kg per day, although Gauthier–Pilters has recorded camels eating 30—40 kg of fresh forage. A camel may cover 20 km in the course of its grazing and when able to range freely camels do less damage to the range than stock that crop more intensively and have small ranges. Their browsing strategy resembles that of the giraffe and it is possible that large populations of the two species might compete in acacia scrub. Otherwise camels are not competitors of domestic or other ungulates. The pastoral ecology of the Sahara nomads and their camels has been studied by Gauthier–Pilters (1961, 1974).



(a)

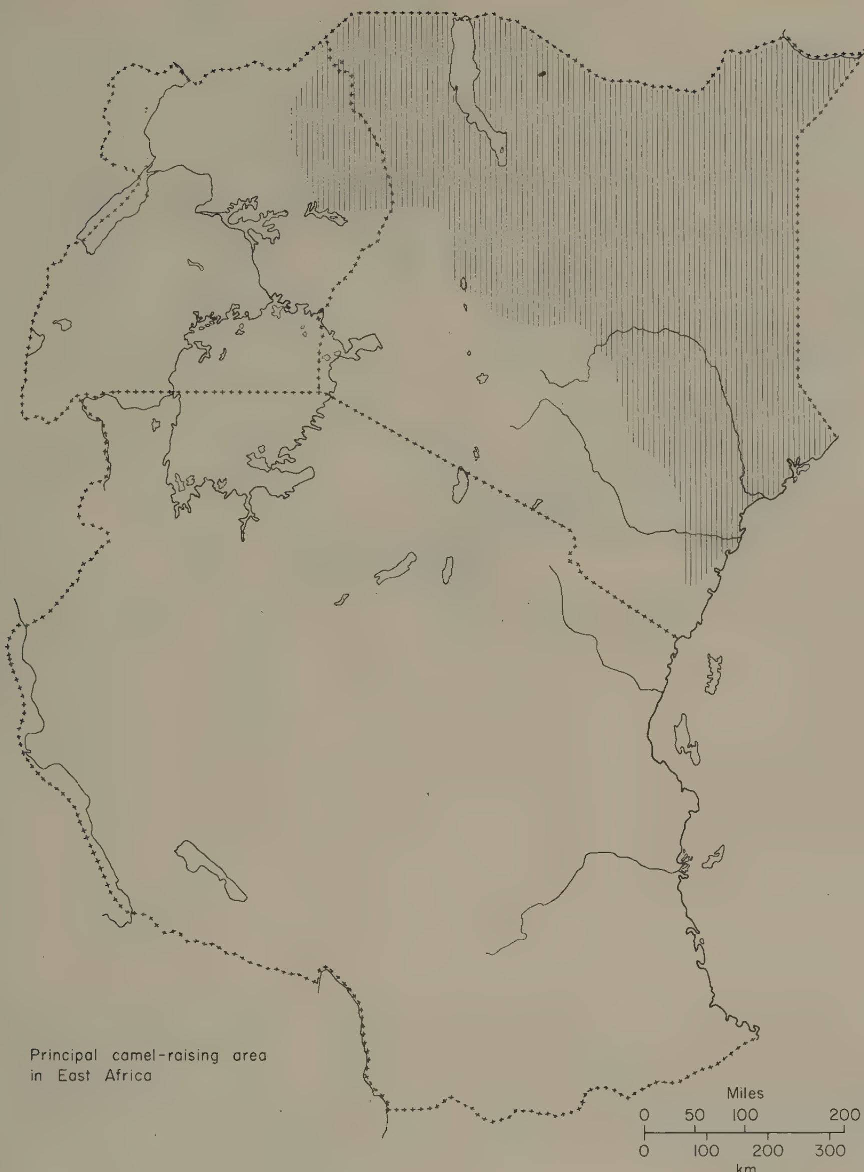


(b)



(c)

Stomach of camel (b) compared with more advanced ruminant (c) and with normal mammalian stomach (a). The latter shows the derivation of the rumen (R) from the cardiac region, the reticulum (ret) from the body and the omasum (o) from the lesser curvature; the abomasum (ab) represents the pyloric antrum. (After Young, 1962.)



The herdsmen and their dromedaries use three types of range in the Sahara and both food and water consumption vary considerably with each of the pastures. During the driest period of the year (May—September in the Sahara) most of the camel herds are concentrated within 50 km of water but they can use pastures up to 80 km from the nearest well. During the cooler parts of the year they can range even more widely as their forage, which may contain up to 30 litres of water, may be moist enough for them to forego drinking altogether. Free-ranging camels feed at night and are often in better condition than their herded counterparts, which are hobbled or otherwise restrained for the night. Gauthier–Pilters suggested that mineral deficiencies might be avoided by the wide variety of forage. Like other ungulates they are attracted to salt licks and some free-ranging herds are conditioned by their owners to find salt at collecting points where herding can be facilitated.

In Kenya the amount of time that camels can spend feeding is decreased with the distance the herds have to travel from the herder's base. Sato (1977) recorded treks averaging 26·6 km a day from the home villages whereas only 15 km were travelled from temporary camps on seasonal grazing grounds. In either case the activity period was about eleven hours.

Scent is especially important to the camel's social life as both sexes have two large glands at the junction between the back of the head and the neck. The deposit from these glands is black and pungent and the head is frequently arched back and rubbed on the back so that the hump becomes well scented. Members of the flock tend to distribute and share one another's scent. They may frequently rub themselves against buildings or tree trunks and roll in mud or soft sand. Camels are easily alarmed by unusual sights and, like equids, they run in densely packed groups when frightened, which avoids dispersal.

In the Sahara, herdsmen have to accommodate the management of their camels to the animal's social system. In some regions of the Sahara, notably Tibesti and Tripolitania, herds of camels are left to range freely for up to five months of the year. Because the camels are entirely dependent on humans for water from the deep wells and because the traditional grazing and watering points are not too far apart in these areas, their owners can manage their herds in a semi-wild state (Gauthier–Pilters, 1974). Small groups of

unguarded camels will join up freely to form larger herds. When walking in single file, such mixed groups are generally led by an elderly female. Small nursery herds and bachelor groups can be seen while some of the old males as well as the occasional female with her young may lead fairly solitary lives.

Between December and April the dominant males become very aggressive towards other males and occasionally towards humans as well, so the pastoral nomads avoid the males continually fighting over possession of the females by dividing up their flocks, leaving one male to about thirty females.

In a wild state, breeding groups were perhaps smaller than this, as the nomads simplify some of the management problems contingent upon rutting behaviour by castrating a proportion of the males. Dominant males are less intensely aggressive towards the gelded animals, which are castrated before the "rutting age" of six years but some three years after sexual maturity at the age of two.

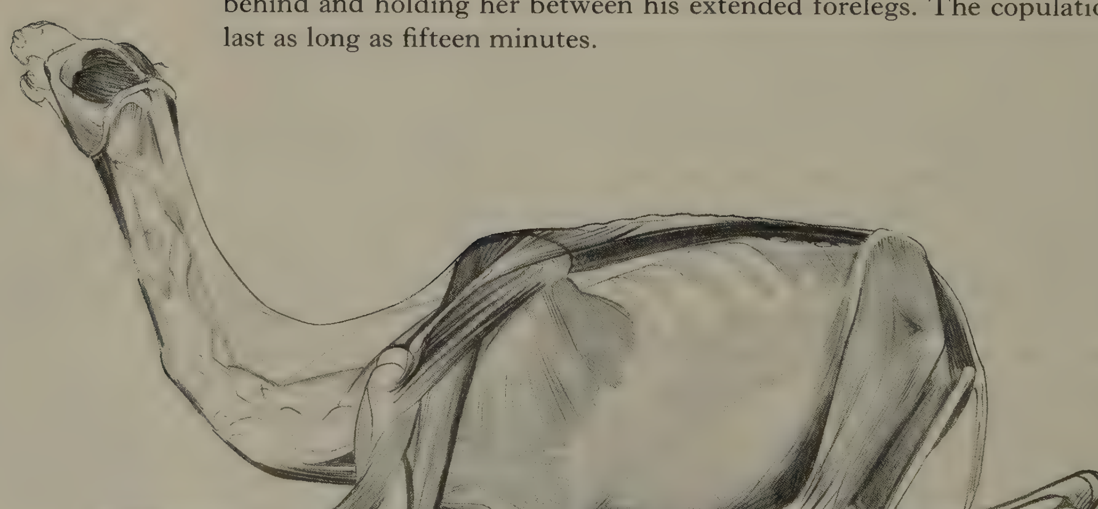
Male dromedaries excluded by the seasonal intolerance of dominant males are herded together and these groups are tolerated by the harem males up to a distance of about 50 m from their females but any bachelor approaching closer than this is driven off. (Bachelor groups have been observed in wild Bactrian camels.)

If two rutting males come within sight of one another while in the presence of females they immediately start to display, throwing their necks back, rubbing their glands on the hump and blowing up a soft, inflatable skin that covers the back of the palate; this protrudes from the mouth, thus crowning the animal's display with a bright pink balloon. Each male makes a gobbling noise, gnashes its teeth and lashes its tail up and down as it defaecates and urinates vigorously.

If an intruder approaches and neither animal breaks off there is a very noisy and energetic fight, in which the struggle seems primarily directed towards upsetting the opponent's balance and pinning him down with the neck and chest and then choking him with the pressure or by biting at the throat. Bites can be directed at the legs, testicles, neck and hump; the sharp short canines are capable of inflicting wounds and there are occasional fatalities. Fights and displays can break out at any time of the year but are most frequent during the rutting period, which reaches its peak in February and March in North Africa.

In Somalia and northern Kenya the rut is known as *Waghogh* and occurs in April—June or September—November. Seasonal and local variations in the quality of fodder during the rains were thought to influence the duration of the rut (Leese, 1927). This author also reported that rutting behaviour is suppressed in a male that loses a fight and that within a male herd only one or two dominant individuals maintain their rutting displays. These animals are very restless, their appetite falls off and it is likely that the rut is terminated by exhaustion and loss of condition.

A courting male directs some of the intimidating gestures of the former display towards a female, showing his bright pink bubble of inflated palate skin and gobbling while he rubs his gland on the hump (this memorable display is beautifully portrayed in some of the funerary pottery figures of Bactrian camels made during the T'ang Dynasty in China). Intimidation may be a necessary element in courtship as the female submits to copulation after being forced into a seated posture; the male then mounts her squatting behind and holding her between his extended forelegs. The copulation can last as long as fifteen minutes.

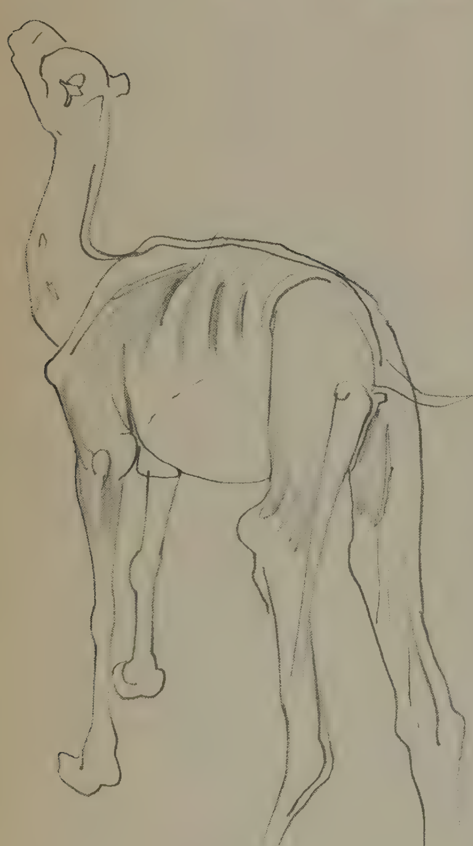


Gestation lasts between twelve and thirteen months and a female has one, or very rarely two, young every other year. Calving and mating coincide with a flush of desert growth and the breeding rhythm appears to be rather fixed; Sudanese camels have been found to cease reproduction when transported from a region of winter rains to one of summer rains.

Once the mating and calving periods are over, the violent intolerance of the males diminishes and the herds can aggregate as the drought worsens.

The young dromedary uses its voice from the moment its head comes out of its mother, which gives birth lying on her side, and recognition between dam and young may be principally vocal. Bonds between the mother and her young are not close; for example, there is little or no mutual licking and the young spend most of the time in groups of their own. The young are precocious and Gauthier–Pilters (1959) has recorded the first appearance of various characteristics. They stand in less than two hours and can run and walk before the second day. Lactation can last for up to twenty months, although a young camel starts eating vegetation before it is two months old.

The milk is a very important part of the desert nomads' way of life and a camel mare in full lactation can produce up to 4·5 litres a day. The milk is commonly made into cheese and fermented into a kurmiss beer. The meat of surplus males is traditionally eaten to celebrate special occasions or to avoid starvation. Where market rather than subsistence economies have prevailed, camel meat has retained a high value, fetching relatively high prices in Kenya, where the principal buyers are Somalis. For truly nomadic peoples the camel herds provide most of the needs of subsistence for a maximum number of people; the wool and leather for tenting, rugs, shoes, straps and clothing; dried dung is fuel for fires and the animals themselves are both pack and mount animals.



In an investigation of the ecology of Rendille camels in northern Kenya, Sato (1977) found that these desert people are so completely dependent on their camels for food that they must time their marriages and age-set systems and even manipulate their own male population growth to synchronize with the population dynamics of their camels. The animals provide a daily average of 686 g of milk per person in a Rendille village (about two persons per milch camel) so that a man starting a family must own a sufficient number of she-camels to provide continuous and reliable food; also he must pay a bridewealth of four she-camels and four males. Female camels reproduce at the age of five years and are fertile for 20 years. The Rendille camel population grows at about 3·2% in spite of infant and juvenile mortality being over 15% (mainly from disease). Sato estimated that the female camels that are given to a boy at his birth, at circumcision and at the tooth-drawing ceremony only

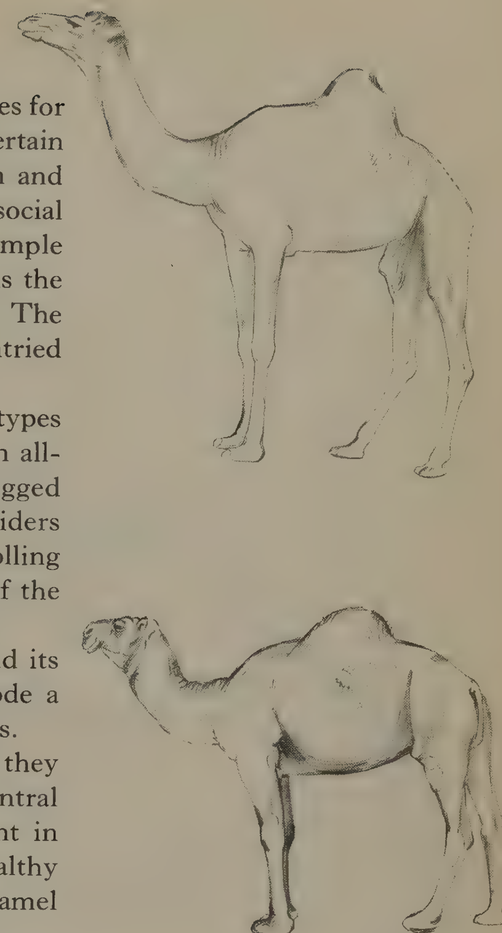
multiply about one and a half times in fourteen years so that the resources for his marriage are not provided for until he is over 31 years old. Certain daughters are not permitted to marry before their brothers; abortion and infanticide are also practiced and Sato regarded these customs as social adaptations to the slow growth of the camel herds. Cultural change has simple implications for the Rendille; so long as they are dependent on camels the abolition of their harsh traditional custom must lead to starvation. The alternative is to abandon their dependence on the camel and adopt untried sources of food, new technologies and unfamiliar livelihoods.

In Arabia and North Africa, selective breeding has resulted in types suitable for carrying heavy baggage, riding in races or cavalry or as an all-purpose animal. The riding or "Mehari" camels are particularly long-legged and slender and are capable of covering up to 80 km per day, allowing riders to reach destinations 500 km apart in less than a week. Because of the rolling gait most novice riders of camels feel distinctly sick on these "ships of the desert".

Wars and other human affairs often test the camel's endurance and its ability to stand heat and lack of water, as when General Gordon rode a camel over 250 miles of one of the worst areas of the Sahara in 50 hours.

Dromedaries were once used more extensively in East Africa than they are today, and Somali cattle traders brought them as far south as central Tanzania and Dar-es-Salaam. Nonetheless, camels are very abundant in northern Kenya and, because this area is well suited to the breeding of healthy camels, it has been suggested that Kenya could develop a successful camel bloodstock trade with less well-endowed areas of the Middle East.

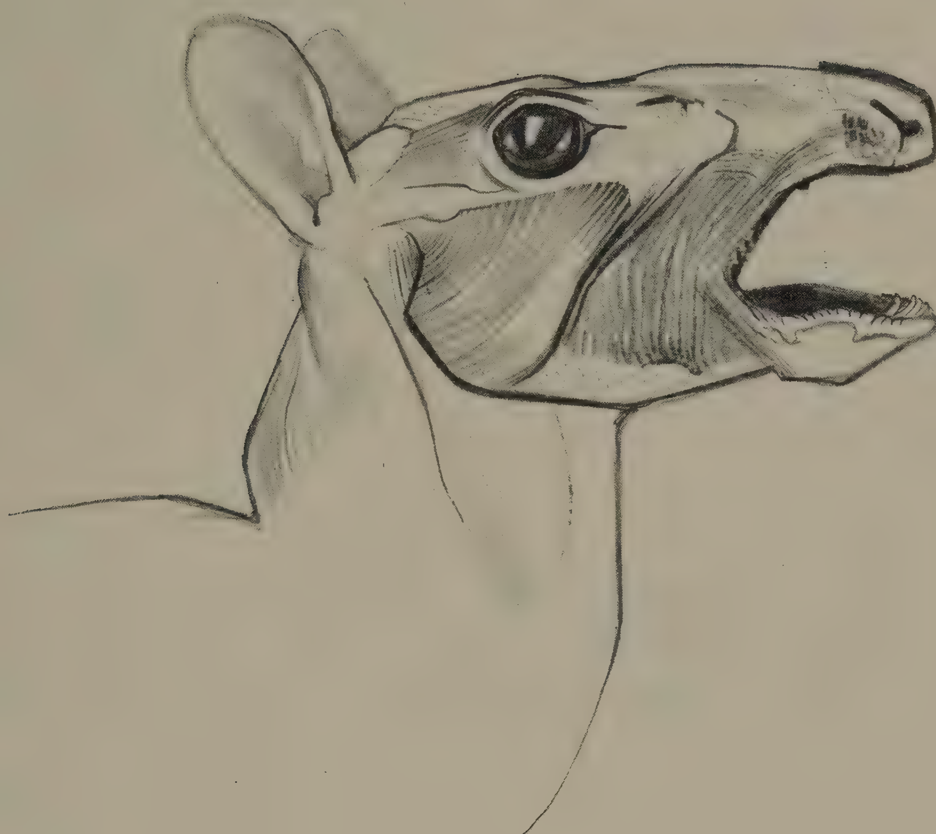
Dromedaries have been introduced into Australia, Spain, central America and South-west Africa and have become feral in some localities. They are capable swimmers and in southern Spain, feral camels lived for 120 years in the marshy delta of the Coto Donana, showing that they can adapt even to areas of seasonal swamp. Old males acquire massive dimensions and with care a camel will live for fifty years.



Camels bred for different purposes. Below: heavily built pack animal; Above: slender riding camel.

Chevrotains

Tragulidae



It is rare for primitive relics not to be highly specialized—yet the chevrotains have remained typical tragulids and they exemplify a family that was abundant in the Old World from the late Eocene to the Miocene.

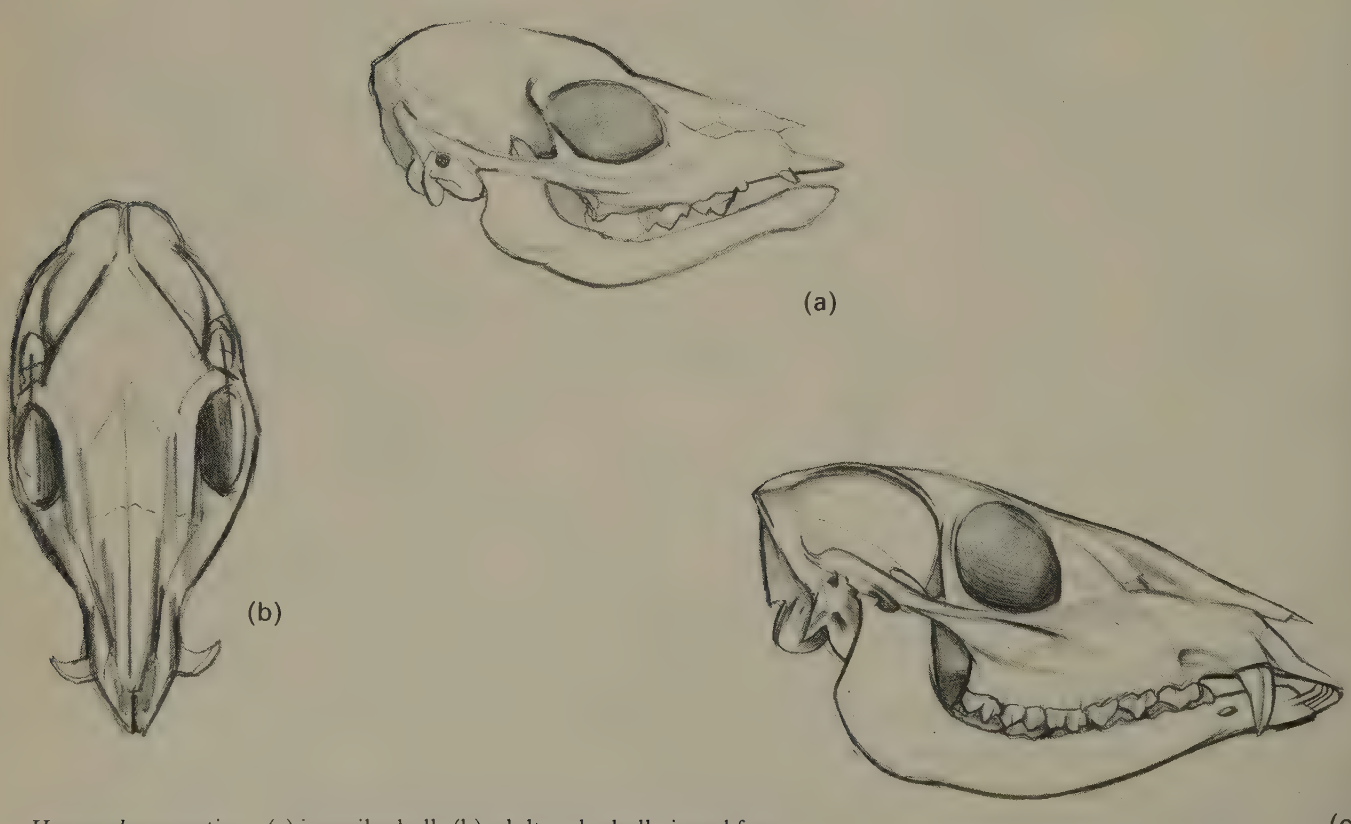
They have lateral toes and short metacarpals like pigs and their behaviour also shares some primitive features with the suids (see Dubost, 1964a, b). While the pigs continued to diversify and evolve, the once varied and widespread tragulids are now represented by a single genus in the Oriental region and another monospecific genus in Africa.

The reason for the chevrotain's conservatism may be linked with the distinction of belonging to the generalized ancestral stock of deer, giraffes and bovids. Whereas suids were able to expand into a variety of rootling niches, the progressive radiation of higher pecorans, particularly bovids, eventually filled every herbivore niche and blocked almost all possibilities for specialization.

However, the chevrotains had the advantage of a long head start in adapting to the peculiarly stable environment of the equatorial forests and a paucity of herbage under the canopy favours an animal with a catholic diet while it puts restrictions on the more efficient but less versatile bovids.

In such conditions extreme conservatism over a period of twenty million years seems to have been sufficiently advantageous to allow chevrotains to survive in the principal Forest Refuges of Africa and even to be moderately numerous in some localities. In this instance the equatorial forests have sheltered a very early type of ruminant and the details of its anatomy, physiology and behaviour illustrate and illuminate the progress of evolution in a way that no fossil can.

Chevrotains have long been the subject of intense interest for comparative anatomy (Milne–Edwards, 1864; Boas, 1890; Pocock, 1919; Dubost, 1964—65; Langer, 1974) and more recently for comparative ethology (Dubost, 1965; Ralls, 1971).

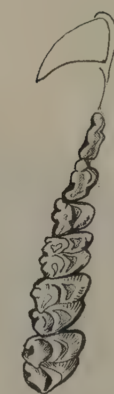


Hyemoschus aquaticus : (a) juvenile skull; (b) adult male skull viewed from above; (c) adult male skull, side-view.

The retention of sharp canines and lack of ritualized modes of combat have considerable implications for the ecological success of chevrotains because the spacing of males is settled by direct confrontation and elimination of the weakest. The apparent absence of scent glands and marking behaviour also reduces the efficacy of mutual avoidance behaviour and probably increases the spacing of individuals beyond the optimum for reproductive and nutritional efficiency.

They have considerable potential interest for studies in comparative physiology (Noirot–Timothee, 1968).

The fossil tragulid with the greatest resemblance to *Hyemoschus* is Miocene *Dorcatherium*.



Right upper toothrow

Water chevrotain (Hyemoschus aquaticus)

Family	Tragulidae
Order	Artiodactyla

Measurements

head and body

74 (60—85) cm

Average 72·5 cm males

Average 76·8 cm females

height

35 (30—36) cm

tail

12 (7·5—15) cm

weight

7—15 kg

Average 9·7 kg males

Average 12 kg females

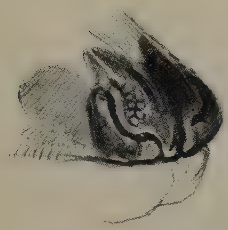
Water chevrotain (Hyemoschus aquaticus)

The water chevrotain is compactly built with a rather short neck, a small narrow head and relatively inconspicuous ears. The limbs are short in relation to the length and bulk of the body but the hindlegs are very powerfully muscled.

The African chevrotain has white dorsal spots, some of which amalgamate along the sides to make a longitudinal stripe or stripes, while the throat and chin bear a bolder pattern of black and white markings. This pattern can be seen with little modification in the Oriental *Tragulus memnina*, which suggests that these animals share their common Oligocene ancestor's coat pattern. However, spotted stripe patterns turn up on the young of such totally unrelated groups as tapirs, pigs and deer as well as on the tragelaphine antelopes. Indeed, even the young of grebes, coots and some gallinaceous birds have similar markings. Portman (1952) regards these immature, early phases as patterns of "lower rank" than the mature phase, and it is clear from the numerous pictorial reconstructions of extinct animals that such markings are widely regarded as primitive. All these diverse animals and birds have in common the habit of "freezing", at least during this early colour phase, and it is most likely that such elaborate patterns have a survival value and are closely correlated with vulnerability to predators. For some species this vulnerability declines as the animal matures and social and other considerations may demand a different coat. For others there are no such pressures and there may continue to be advantages in a cryptic coat, particularly if the adults continue to rely on "freezing" to escape attention, as is the case with the chevrotain.

One aspect of the chevrotain, however, is not cryptic at all and that is the throat. When the head is raised a bold black and white pattern is revealed and the hair in this region is much coarser in texture than the rest of the body fur, which is relatively soft and sleek. This throat hair is underlaid by a zone of specialized tissue between the skin and the well developed superficial muscles, the effect of which is to thicken the neck. Since the pattern begins at the corner of the mouth the head, which is already small, appears poorly differentiated from the neck. Facial expression and "ear signalling" seem to be undeveloped so that the orientation of the neck and carriage of the head as well as general body postures may be important means of communication. If the subdermal tissue of the neck is glandular, chevrotains might gain olfactory information about one another by smelling or licking this region.

Primitive animals tend to survive best in habitats that are: (a) sufficiently rich in food resources to reduce competition, (b) sufficiently difficult for predators to miss a high proportion of their potential prey, and (c) sufficiently stable ecologically to give an advantage to older adapted forms. The low-lying African Forest Refuges (see Volume I, pp. 28—45, 63—67) fulfil the first and the last of these conditions, while the swampy areas and stream beds within these forests fulfil the second (see Volume I, pp. 31—32) and it is in these areas that the chevrotain lives; similar considerations apply to

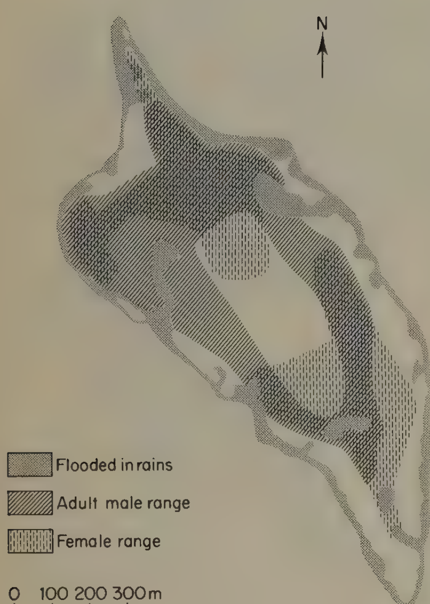


Tragulus memnina in Asia, but the latter appears to tolerate much drier habitats than the semi-aquatic African chevrotain.

Within the lowland forest biome the margins of streams and swamps are an ecologically varied and rich environment with a wide range of available foods for omnivorous animals and it is these resources that the chevrotain exploits. The main item of food is probably fallen fruit, of which the following trees are important sources: *Pseudospondias microcarpa*, *Ficus* spp., *Treculia* and *Elaeis*. In the undergrowth, *Calamus*, *Aframomum* and *Marantochloa* fruits are eaten and Malbrant and Maclatchy (1949) list other fruits eaten in western Africa. Aquatic plants, lily roots and grass have also been reported and Rahm (1966) adds the leaves of *Galinsoga parvifolia*. Dubost (1963) noted that insects and crabs are caught and eaten and scavenging habits are betrayed by the presence of boneless meat, liver and fish in the stomachs of shot chevrotains. He described captives chewing in the manner of a carnivore when given a large piece of meat.

While investigating its surroundings the chevrotain actually pushes the vegetation aside with its peculiar snout (see drawing above, left) and must rely extensively on its sense of smell to identify food. This species of chevrotain appears to be predominantly nocturnal and crepuscular, while the smaller Oriental *Tragulus javanicus* is reported to be intermittently active throughout the day and night.

In Gabon, Dubost (1978) encountered chevrotains foraging in exposed clearings, on flood plains, open river banks and sandy flats at night but never found them outside their forest hideouts during the day. Dubost demonstrated that the nature of these diurnal resting places was determined by the frequency of rain by correlating his monthly records of resting sites with the number of rainy days.



Chevrotain ranges on a forested island in Gabon. (After Dubost, 1978.)

Month	Exposed resting site	Resting site at the foot of a tree	Sheltered resting site
April (15 rainy days)	0	0	5
May (12 rainy days)	0	2	7
June (7 rainy days)	3	1	3
July (3 rainy days)	3	1	5
August (4 rainy days)	3	0	2

Chevrotains are physiologically adapted to a fairly narrow range of temperatures and avoid extremes, in fact prolonged exposure to strong sun can kill some individuals (Dubost, 1978).

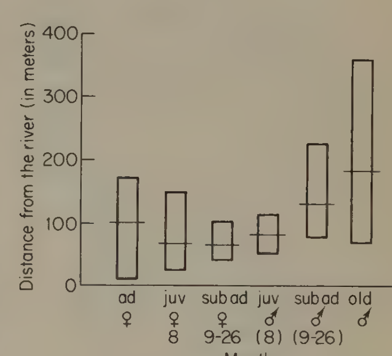
This species' need for water is both physiological and behavioural in that rivers and swamps provide a refuge from predators. The rainy season sees a superabundance of fruiting trees throughout the forest and Dubost (1978) has noted that this favours the dispersal of chevrotains, particularly males which tend to abandon the family units at the beginning of the rains. During the dry months chevrotains concentrate along permanent water courses where nutritional needs and refuges are met more readily.

The chevrotain's walk is not dissimilar to that of a short-legged duiker; it will sit on its haunches like a pig and then lie down folding its forelegs

under the body. It prefers this resting posture with back arched to lying on its side, which it rarely does. It is reported to clamber into tangles of vegetation and up sloping tree trunks—like some of the duikers—and it can make a short fast spurt to get away from an enemy, and Dubost (1968) describes it making jumps like a rabbit. Although water is the chevrotain's major refuge from enemies the animal is not adapted to long periods of immersion nor to sustained swimming. It can dive and progress under water for some tens of metres but its relatively clumsy dog-paddle is so wastefully energetic that the animal soon tires.

The use of dogs for hunting reveals traces of chevrotains that would otherwise escape attention and I have been led to their well-hidden resting places by small dogs. However, they frequently travel over established pathways, particularly along valley bottoms. When alarmed they are reported to rush for the nearest river and submerge, swimming upstream and coming to the surface beneath banks or overhanging vegetation. This is perhaps their last resort, after having been dislodged from their "form" or detected while "freezing", which is their first line of defence.

In his study of the ecology of the chevrotain Dubost (1978) thought that their spatial distribution was determined by the need to be within a short run's distance from an aquatic refuge and he noted the animals' absence from areas away from rivers. He determined however that the distance of diurnal resting places from the water varied according to sex and age (see fig.). He also noted that density was not only influenced by the abundance of their principal food, fruit, and the presence of rivers but by the availability of dense tangles and hollow tree trunks to lie up in and he found that chevrotains were very irregularly distributed in Gabon with densities of 7·7 to 28 animals per sq km. By capturing and recapturing some individuals and radio-tracking others, he discovered that adult females lived in an area of 13—14 hectares all their lives and that they were spaced at an average of more than 450 metres from each other. Males on the other hand occupied 20—30 hectares and were never found in the same place for more than a year (it was not known what happened to them).



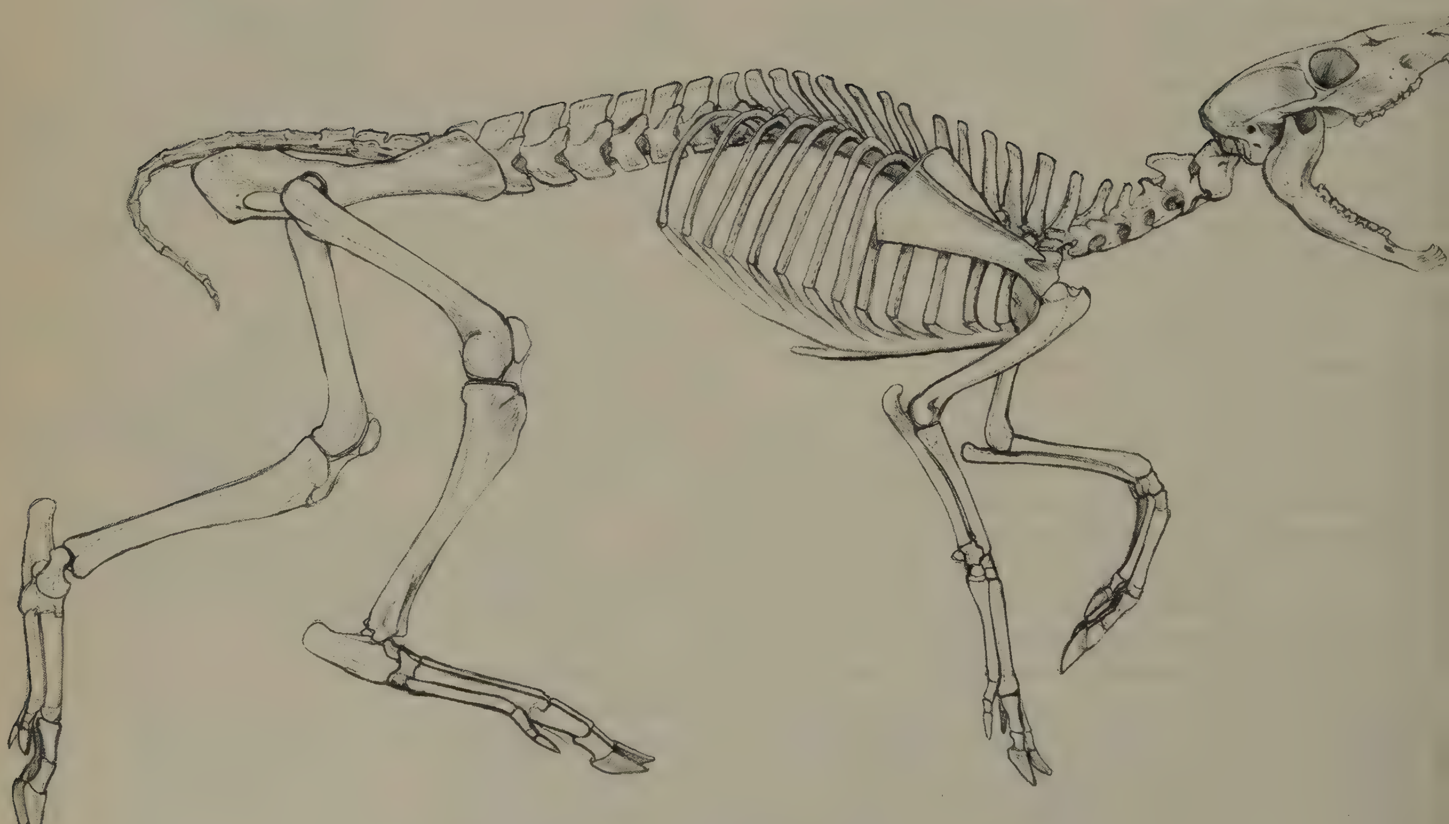
Distances of chevrotain resting places from water classified by social categories. (From Dubost, 1978.)

In Ceylon, Eisenberg and Lockhart (1972) sighted an individual female *T. memnina* on several occasions in the same locality and they concluded that although the chevrotains moved about on their own, several individuals used the resources surrounding a single waterhole and they could be recognized as a "community". These authors also found evidence of the animal's attachment to its home locality by catching desiccated individuals that had failed to move out of their home area during a drought.

When a large tree is fruiting the animal lives in its immediate vicinity and may feed almost exclusively on the fallen fruit—the specimen figured was trapped in just such a situation.

The social system of *Hyemoschus* is rudimentary and somewhat similar to that of a solitary carnivore. Dubost (1978) found the females spaced out in isolated home ranges that are apparently without overlap or contact zones. Occasionally two related females may temporarily share a range but with minimal interaction or contact and Dubost has described their social behaviour as the avoidance of other individuals. The larger male ranges may embrace two female ranges within them. Measuring affinity in terms of

average spatial intervals, Dubost found that the older males were spaced out up to several kilometres apart but that younger males tended to cluster around a female or mature male range with average intervals reduced to 267—336 metres. Dubost recorded many of these two- to five-year-old males with wounds indicating that competition between themselves and with older males was intense and contributed to a radical change in the overall sex ratio. There were 45 males to 92 females of reproductive age but males aged five to eight years old never accounted for more than 25% of Dubost's samples. Although longevity is estimated at twelve to thirteen years, Dubost found very few animals over eight years old and these aged animals belonged equally to either sex. According to Dubost fighting is unritualized. The combatants rush at one another with their mouths wide open to reveal the sharp canines and make scythe-like lateral swipes at one another. Long slashes in the side and front of the body are sustained during such fights.



Dissected chevrotain shows exceptionally thick dermal muscles on body and neck. Neck also has thick collar of tissue over muscle.

Dubost and Terrade (1970) described the dense, tough skin and hypodermis of the chevrotain. They pointed out that the connective tissue is composed of very thick fibres which form a dense web covering the upper part of the body and supposed that it serves to shield the animal from mechanical injury in the undergrowth. This could be an important factor, as they will rush rapidly through thickets of *Pandanus*, *Phoenix reclinata* and other thorny or abrasive vegetation, but the fighting technique must be the primary reason for this protective adaptation. Beneath the skin of the throat there is a collar of dense tissue which may be glandular but might also serve a protective function. In addition to this the superficial muscles of the neck (*trapezius*, *cleidomastoideus* and *panniculus*) as well as the dermal muscles covering the flanks are exceptionally thick, a hyperdevelopment that seems to be associated more with increasing the depth of the shield than with movement or skin twitching.

The tushes are also used in defence and I was shown a scar on a hunter's heel which was claimed to be the work of a male chevrotain caught in a pit-trap. Eisenberg and Lockhart (1972) also reported *Tragulus memnina* jerking its head to one side and kicking when handled. The sharp hooves can also cut deep wounds.

Chevrotains are not sufficiently numerous in Bwamba to be caught with great frequency but they are reputed to be locally abundant in swamp forests in Zaire and West Africa. Sidney (1965) says they are an easy prey of the night hunter, presumably meaning that they are susceptible to dazzling by torch.

The exceptionally wide spacing of male chevrotains appears to be the product of intense fighting eliminating any possibility of contact zones. The smaller size of males may reflect the need to reduce risk to the females. Local hunters and authors have remarked on the striking difference between the sexes in temperament, the males being more nervous, active and aggressive. While competition for the females may influence male spacing, it is likely that the females are also mutually intolerant and that the fragmentary dispersal pattern of chevrotain populations may be partly a primitive characteristic and partly a mechanism to avoid intra-specific competition for food. However, the chevrotain is also likely to suffer competition from other animals, particularly pigs, duikers and chimpanzees. When a group of young chimpanzees was released on the island where Dubost was studying chevrotains the central area of the apes' activity was abandoned by the chevrotains altogether. The restricted and artificial nature of this intrusion makes it as likely that physical disturbance was as important a factor as competition but the chevrotains' response illustrates that their occupancy of an ancient niche is tentative and fragile.

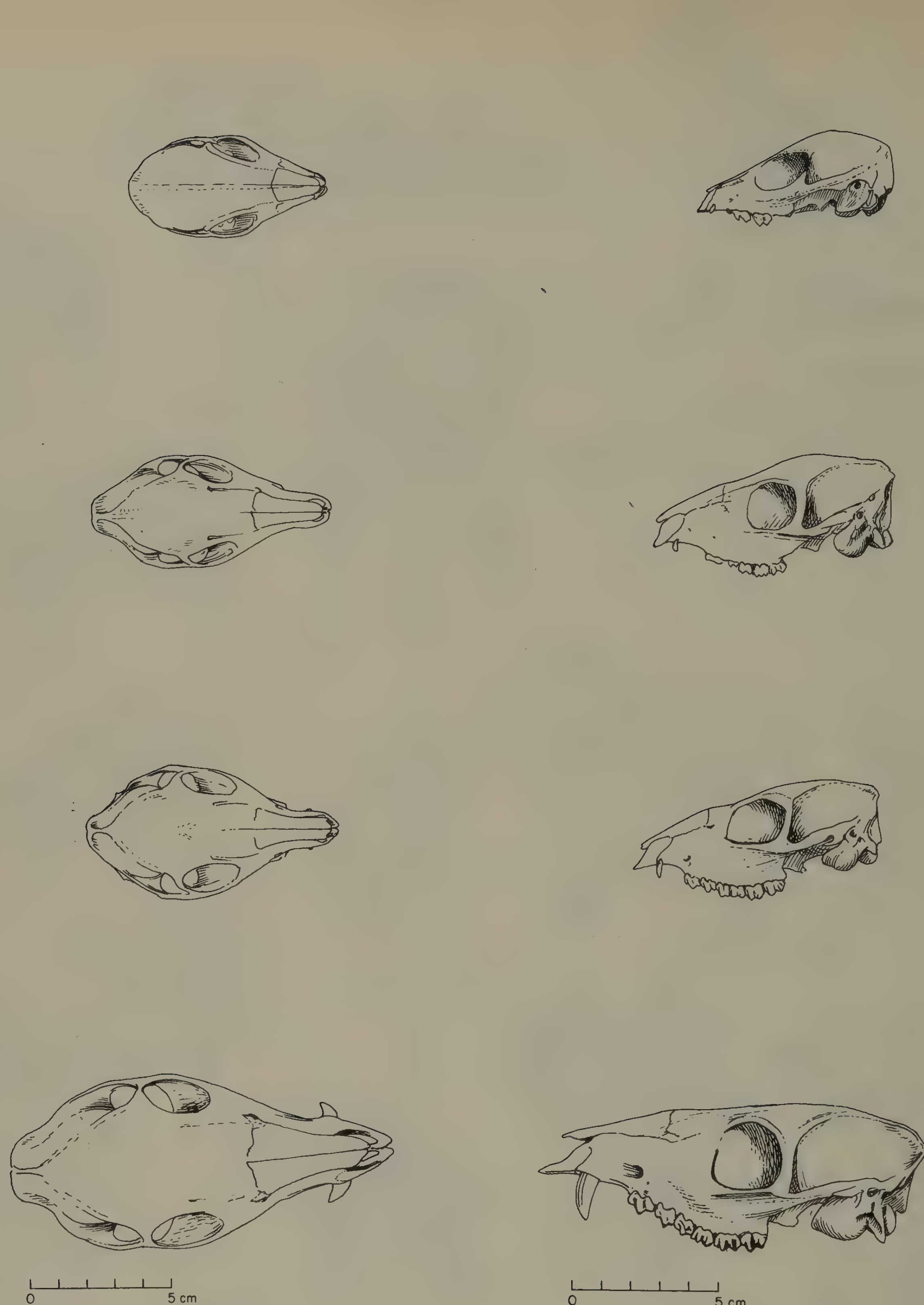
It is possible that in some areas of West Africa selective killing of the large duikers and pigs may thereby increase the food supply of the chevrotains.

The chevrotain's courtship has been described by Dubost (1965a). Once a female comes into oestrus it is followed by the male, which utters a series of brief cries through its closed mouth. At each cry the female stops instantly as if by reflex and lowers her head. The male can then approach and lick her genital region, whereupon she walks on. This sequence is repeated and the duration of the courtship depends on the level of excitement shown in both partners. Finally the male mounts, laying his head and body over the length of the female's back. Males have not been seen to test urine or to curl their upper lip.

The gestation period has been reported to be 120 days (Walker, 1964) but the smaller *T. javanicus* has been timed at 152 days (Davis, 1965), and the normal gestation of *Hyemoschus* is more likely to be in the region of five to six months.

In eastern Zaire two full-term foetuses have been recorded, one in mid-April and one at the end of July. The latter measured 260 mm overall, 50 mm of which was tail. One young is born at a time but females have four mammae, which implies a capacity for bearing more than one young.

In captivity, *T. javanicus* gives birth throughout the year and the young are precocious, standing in half an hour and beginning to eat solid food at about two weeks. Weaning is completed by three months and both sexes are capable of breeding at four-and-a-half months. *Hyemoschus* is a larger animal and the young lie up and are relatively inactive during the first three months of life, being nourished almost entirely on milk sucked during the periodic visits of the mother. The dentition is wholly deciduous until the first molar appears between the fourth and ninth months, a period in which



there is rapid body growth and increase in activity. The juvenile is weaned by the age of nine months and at about this time the animal can become sexually mature. According to Dubost (1978) there is considerable variation in the age of sexual maturity with ranges from nine to nineteen, even to

twenty-six months. The second molar erupts and becomes functional between ten and nineteen months, a period of continuous growth and the beginning of avoidance of adults.

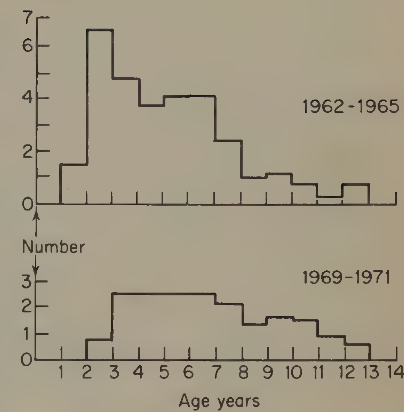
The third molar appears between the twentieth and twenty-third month by which time adult dimensions have been reached but weights are inferior. It is during this period that the animal is most mobile. With the completion of the adult toothrow, Dubost assessed age on the basis of wear of the last outer cusp or metacone of the third upper molar.

By recording the ages of all females that were pregnant or lactating, Dubost (1978) was able to demonstrate the effect of intensive predation on reproduction and population structure. The figure opposite compares these records before and after a marked intensification of hunting pressure at Makokou. Hunting hits the younger and most fertile animals hardest, reduces total reproduction, disturbs the ratio of sexes and causes incidental mortality in dependent young.

It is very unlikely that this species will continue to survive in East Africa. Its only known stronghold is being subjected to a form of forest management that will entail the destruction of its habitat (see Volume I, Insert p. 47). When I asked for permission to collect a specimen in 1964, the department concerned had decided that there were "no grounds whatsoever for having included this species in previous schedules as it is not found in Uganda". It may perhaps be considered quixotic to express concern for the fate of a species in Uganda whose existence was officially denied for several decades. However, in the case of the chevrotain its survival is linked with that of a distinct people and the ancient forest community of which they are both an integral part.

The specimen figured on these pages was trapped for me by the Mambuti pigmies, who were my mentors and guides in Bwamba. Their encounters with the exploitative world that is bent on destroying their forest home have been bitter. Turnbull (1961) tells how the Belgian colonial authorities in the former Congo set up a resettlement scheme for pigmies on plantations.

> "The result was disastrous, used to the constant shade of the forest, to the purity of the forest water and to its absence of germ-carrying flies and mosquitoes, the Pigmies quickly succumbed to sunstroke and to various illnesses. This problem is widely discussed by the Pigmies, who are determined to go on living as they always have. More than once I was told, with no little insight, that 'When the forest dies we die'."



Total number of births and lactations in a population of chevrotains at Makukou (Gabon). (After Dubost, 1978.)

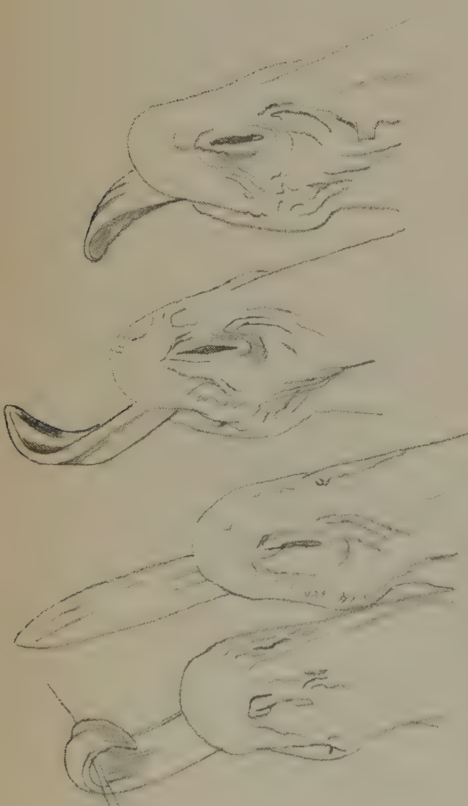
Giraffids

Giraffidae

It was pointed out in Volume 1 that woody growth in Africa is degraded by the combined action of ungulates and fire. These and other factors such as water availability, sunlight, soil, temperature and wind affect canopy height and there is a relationship between humidity and vegetation types which effectively limits the shorter trees of the savannas and acacia bush to climatic regimes with two to nine humid months. The abundance of foliage that is available to browsing herbivores, its distribution and its height are determined, therefore, by a multiplicity of factors and these influence the distribution and ecological success of browsers.

Today giraffes flourish in those areas where there is abundant year-long browse at levels above 2 metres and below 5·5 metres. Foliage above that level is out of reach, while the giraffe is not only clumsy at feeding at low levels but competition from antelopes also reduces its value as a feeding zone. The rare and localized okapi is restricted to a lower and narrower browsing zone in a dense habitat but its niche is similar to that of the giraffe in that its bovid competitors are shorter in stature but fewer in numbers of species.

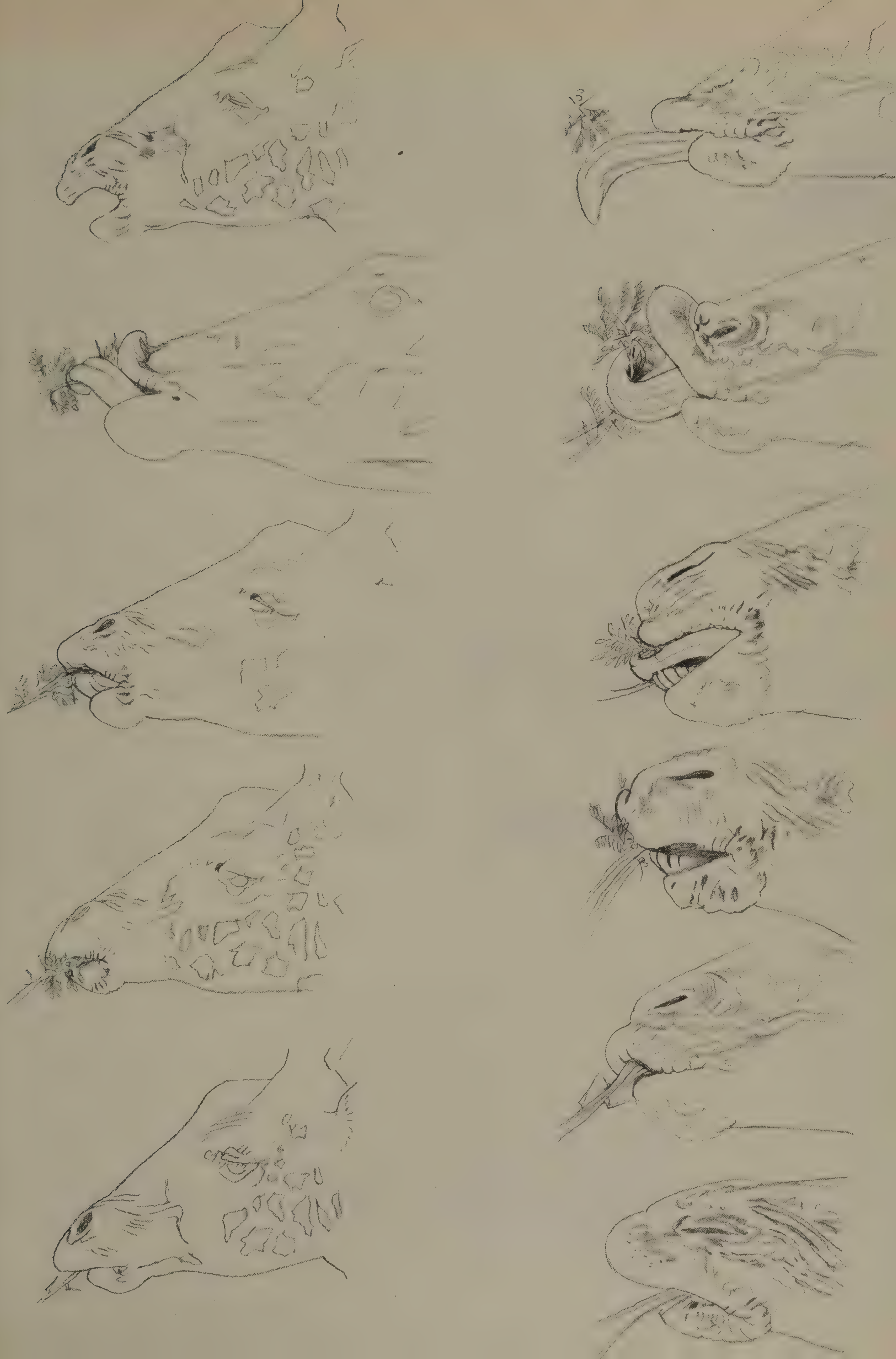
Similar considerations may have operated from the time of the giraffids' first appearance in Africa during the Miocene, for no African giraffid was very small and wherever the proportions of the body are known they appear to have been relatively tall.



The teeth of giraffids are disproportionately small and low-crowned for such large animals and it is clear that the quality of their browse must compensate for quantity. Both the living species have long muscular tongues that are specially adapted to select, gather and pluck foliage. This mechanism is different from that employed by bovids and is capable of great selectivity as well as being exceptionally efficient for stripping fine foliage off twigs (see diagram).

It is very likely that the living giraffe represents the culmination of a distinct specialization that would have begun at lower zones. This specialization was the exploitation of green foliage at levels above those reached by bovids. The giraffe's primary emergence from an early cervid stock was probably in Eurasia, but it is in Africa with its great diversity of competing bovids that the giraffes would have been forced to the limits of their specialization.

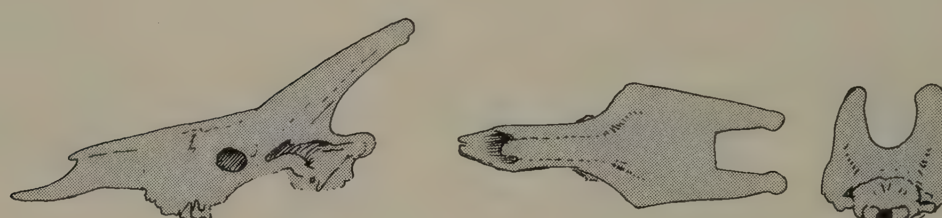
The living giraffe is successful in many different vegetation types, yet several extinct species coexisted in the Pliocene and Pleistocene, which means that the resource that is now monopolized by one species was once capable of supporting two or three giraffids. One was the giant *Libytherium*, another the tall, heavily built *Giraffa jumae* and the other the lightly built *G. gracilis*. While differences in the preferred feeding levels of these giraffes can be predicted there is also evidence from living giraffes as to how size and build might have influenced feeding strategies and niche-separation. Moore–Berger (1974) has found that the shorter females sometimes have to feed on a greater variety of food plants because their feeding zone is narrower and more



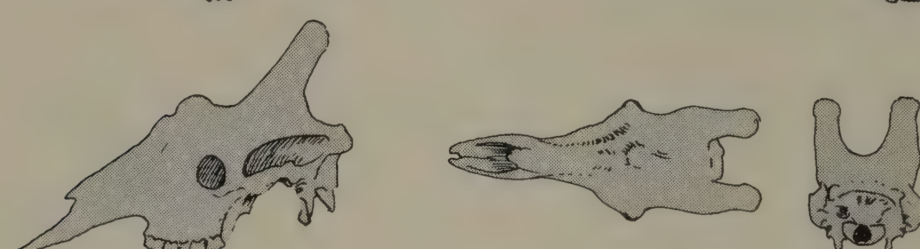
crowded. Slender proportions in *G. gracilis* might have imparted greater speed but they might also imply a more mobile existence.

The long necks of giraffids are not only of ecological significance. Both giraffe and okapi males have much more muscular necks than the females. In their battering contests, in which the bluntly horned crowns are thumped into the opponent's body without matching the head to head, it is the neck, rather than other parts of the body, that provides the motive force. In the okapi, neck fights are common and short jabs from the horns are similar to those seen in antelopes such as the nilghai, *Boselaphus*. In the giraffe, however, the momentum gained by throwing the head over a wide arc is so great that fighting is more like the swinging of a knob-kerry and the male skull has evolved appropriate bony knobs above the eyes and on the occiput as well as growing three prominent "horns". The entire roof of the skull is protected by extensive cranial sinuses and, in old bulls, the eyes and muzzle are capped by a dense layer of rugose bone and thickened skin that eventually dwarfs the features below.

Giraffa jumae



Giraffa camelopardalis.

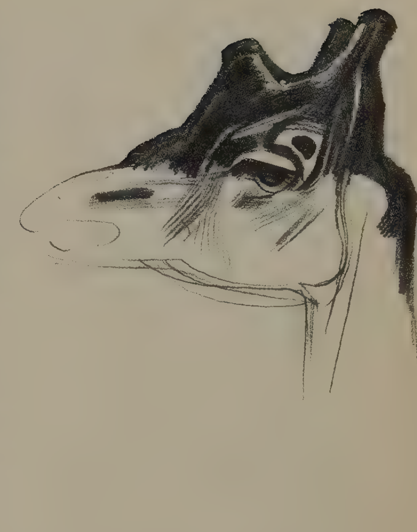


Young males indulge in prolonged ritualized contests in which the opponents stand close together or lean shoulder to shoulder and, swinging their necks to and fro, thump one another in the chest or rump. These rituals are leisurely and may last up to twenty minutes and often include homosexual mounting. Moore–Berger (1974) sees them as serving the establishment of hierarchies within loose bachelor associations. Fully mature bulls, instead, tend to lead a nomadic existence, wandering on their own from one herd to another inspecting females for signs of oestrus. Contests between such bulls are always for a female and are ritualized tests of strength and weight. Movements are more violent and the blows from immensely heavy heads on powerfully muscled necks are unrestrained.

The right of a male to copulate is usually settled after a few blows. In one case where the heads of two fighting bulls collided, one was knocked unconscious, upon which its prone body was further attacked with blows from forelegs (Downey, pers. comm.). Giraffes do not normally use their legs against one another and kicks have only been seen being employed by females in defense of their young against predators.

The arming of the head with bony protrusions therefore serves intra-specific competition between males. In the okapi it is only the male that develops "horns" but the female giraffe horns are without bony reinforcements and they do not develop beyond a stage equivalent to adolescence in the male.

It is interesting that the shorter-necked *Sivatherium*, which may have survived into historic times, had palmate antlers, which implies the opposition of heads, as in cervids. There may have been gradations of fighting style in giraffids since the closely related *Bramatherium* had blunt conical protrusions.



Male showing re-enforcement of crown "knob kerry".

Other attributes of slenderness are to be found in the peculiar gait of giraffes and okapis and in the development of special valves in the giraffe's vascular system. These and other peculiarities are discussed in the profile.

Giraffes may have had a profound influence on tree form, particularly in African species of the Mimosaceae. For example, both *Acacia xanthophloea* and *Balanites pedicellaris* have been found to develop fewer thorns above the level of the giraffes' reach (Moore–Berger, 1974). Ants of the genus *Cremato-gaster*, living in the galls of *Acacia drepanolobium* may also help to limit the damage giraffes inflict on this favourite browse.

Densities of giraffes are very variable but can reach at least six individuals per square kilometre and they are clearly a successful and most economic member of the savanna ecosystem, exploiting a resource that would otherwise be the province of monkeys and insects alone.

Giraffe
(Giraffa camelopardalis)

Family Giraffidae
Order Artiodactyla
Local names
Twiga (Kiswahili and many other languages), Nduida (Kikuyu), Nturga (Kisambaa), Tiya (Kirabai), Tiga (Kalenjin, Lwo), Ndwiya (Kikamba), Etiika (Luhya), Ntegha (Kinyaturu), Hori (Kipare), Ekorii (Ateso), Ndululu (Kihehe), Lenywa (Kimeru), Lment (Samburu), Kanyiet (Sebei), Kuri (Madi), Geri (Somali), Ondere (Lugbara), Salwar (Kiliangulu), Oloodo-kirragata, Olchangito-oodo (Masai).

Measurements
head and body
4·3 (3·57—4·8) m
height (to top of head)
4·25—5·5 m
shoulder height
3 m (2·5—3·7) m
tail
76—103 cm
weight
1,100 (800—1,930) kg males
700 (550—1,180) kg females
Average biomass weight
800 kg
Note: *G. c. reticulata* has slightly smaller measurements

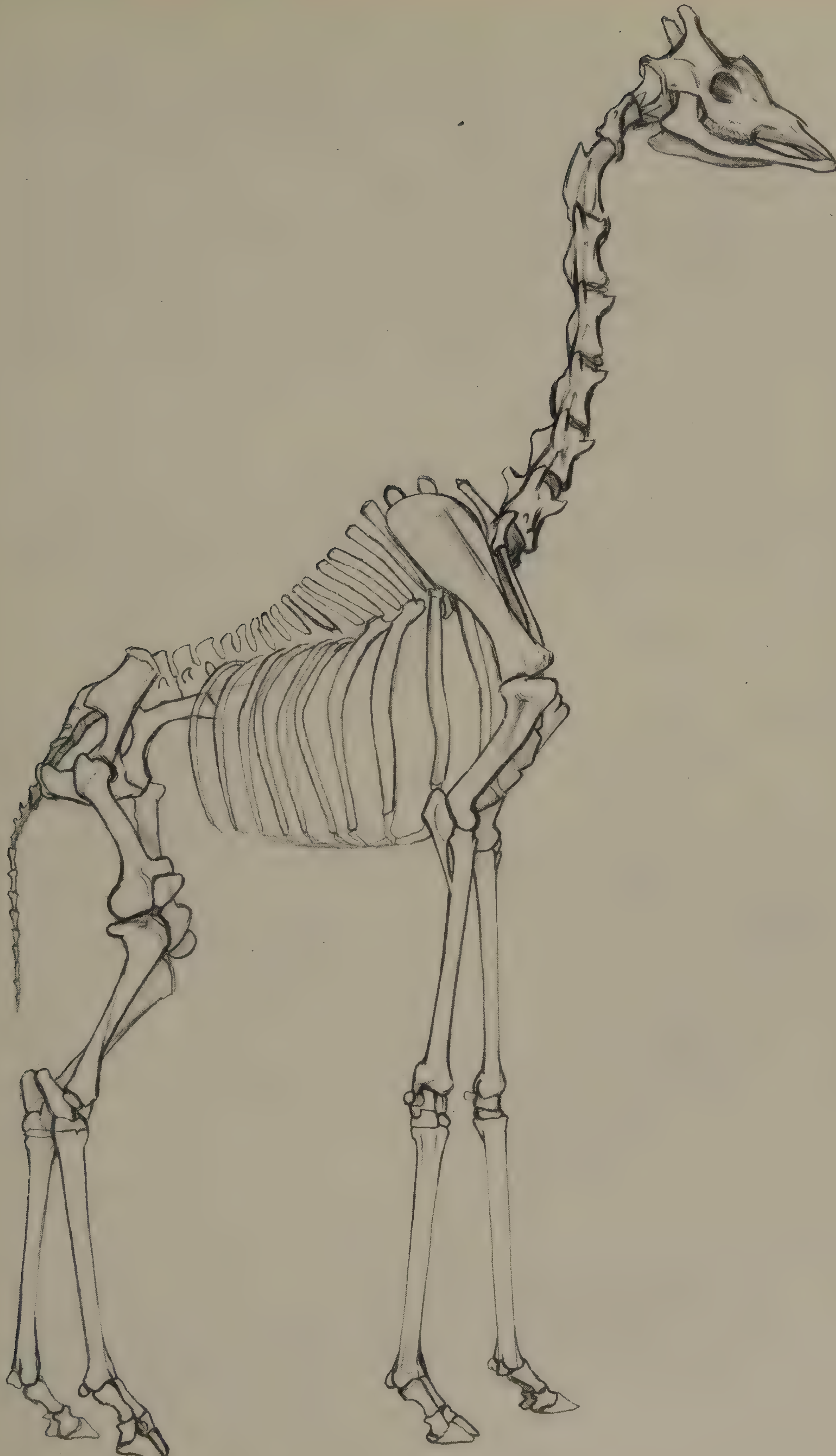
Races

Giraffa camelopardalis reticulata	North-east Kenya
Giraffa camelopardalis rothschildi (Syn. *cottoni*)	West Kenya and East Uganda
Giraffa camelopardalis tippelskirchi	Tanzania and South Kenya

The giraffe's long neck and legs are one of the most dramatic examples of adaptation, the major advantage gained by the giraffe being access to a food supply that is out of reach of all other herbivores. The animal's enormous size has the secondary asset of deterring all but the largest, the most persistent, or the most hungry of predators from attacking adults.

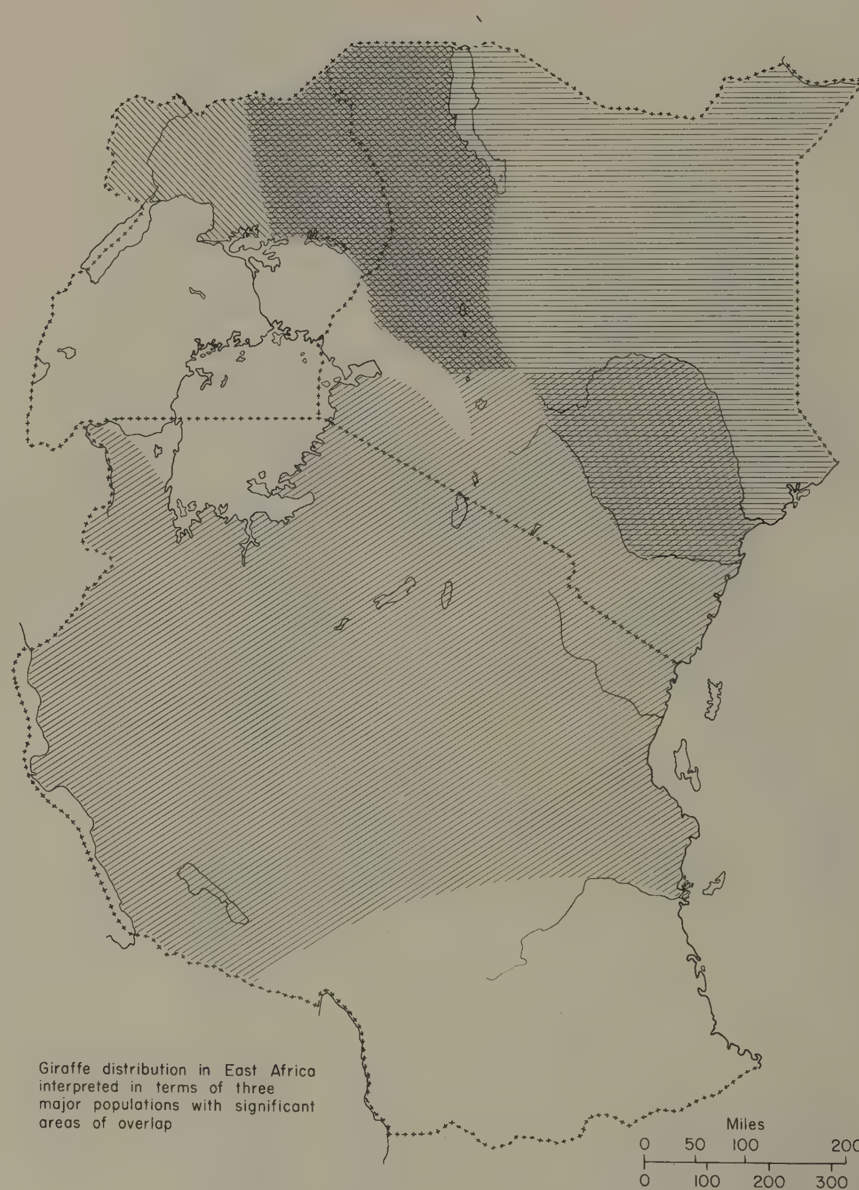
Various theories concerning the evolution of the giraffe's neck are reviewed by Brownlee (1962). This acquisition of a long neck in so large an animal has involved a wide variety of physiological and anatomical modifications. The shoulders are deep and muscular while the thoracic vertebral spines are exceptionally long and carry a powerful nuchal ligament. In order to offset the sudden build-up of blood pressure when the head swings, the giraffe has very elastic blood vessels and valves in the venous system of the neck (Amoroso *et al.*, 1947; Lawrence and Rewell, 1948). Blood pressure changes in the carotid artery have been measured by van Citters *et al.* (1966). These changes do not correspond to the effective height of the fluid columns between heart and head, and these authors believe that an as yet undetermined mechanism regulates the cardiovascular system and compensates for the carotid sinus, which is apparently absent in the giraffe.

Opposite: *Giraffa camelopardalis tippelskirchi* (old male).



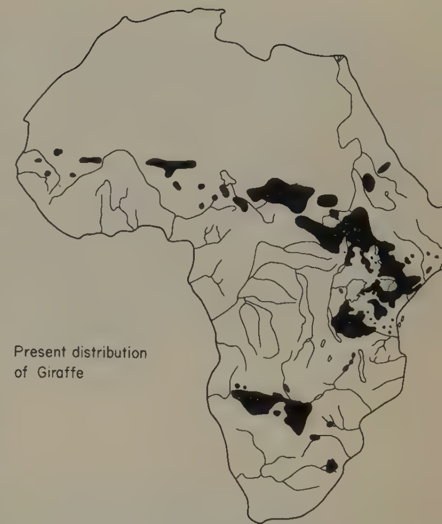
The body proportions of giraffes change with age and at birth the neck is short in relation to the legs. However, the proportions of individuals vary and I have seen an adult with noticeably shorter legs than its fellows. Such individuals exemplify the natural variation by means of which selection works its extraordinary transformations.

The beautiful lattice patterns of giraffes are also subject to considerable individual variation and there is a general tendency towards darkening or towards increasing tonal contrasts in males as they age. Melanistic giraffes have been recorded and one seen at Manyara was jet black and without markings but had a dark tawny belly. White and partially white animals are also known, as well as very lightly coloured individuals with faint markings.

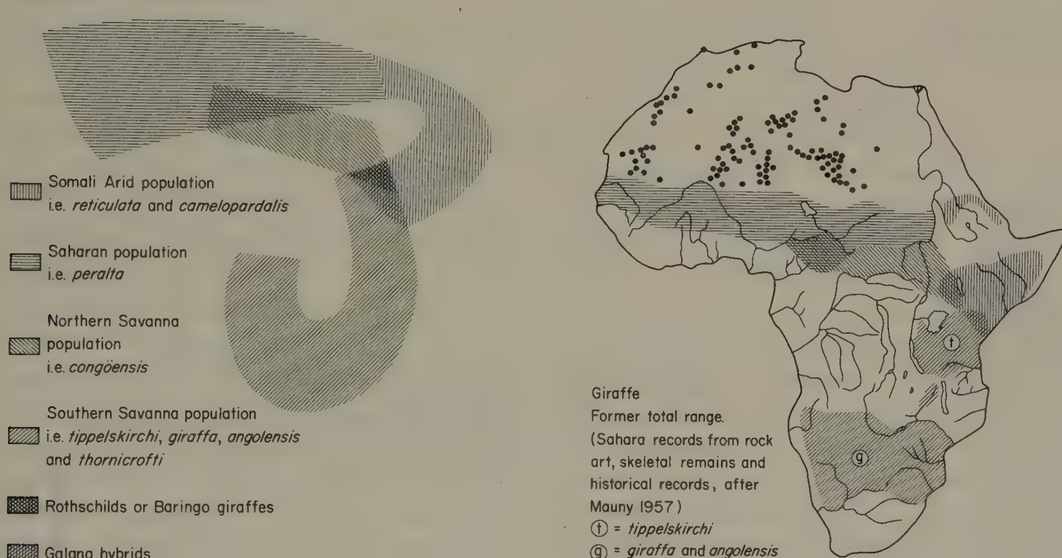


Giraffe distribution in East Africa interpreted in terms of three major populations with significant areas of overlap

It is perhaps not surprising that with such variation in markings there has been a proliferation of names in spite of there being very little difference in the skulls (Singer and Boné, 1960). Four races have been described from East Africa and one, *G. c. reticulata*, has even been treated as a species. The latter population occupies Kenya north of the Tana River and east of the eastern Rift Valley and its pattern represents an extreme development. The dominant dark areas are separated from one another by thin but well-defined light lines. Large dark patches mark the face and extend onto the inner flanks and underparts as well as down the legs, but the hocks are usually light coloured. Two examples are shown in the colour plate.


Present distribution of Giraffe

In contrast to this crisp geometric pattern, the Masai giraffe, *G. c. tippelskirchi*, often has the light tracery dominant and instead of being crisply defined the light areas give the numerous dark patches a jagged outline by apparently "eating" into them. Sometimes the effect is to create an irregular star or cross with a dark centre. This pattern type is typical of the southern savanna giraffe as a whole but the spots of *G. c. giraffa* have firmer outlines. Animals in the northern hemisphere all have better defined patches than their southern counterparts but they are divisible into at least four distinct populations (see map).



Diagrammatic interpretation of the distribution of giraffe populations.

The present distribution of giraffes shows an enormous gap between the southern form in Angola, *G. c. angolensis*, and the woodland population in northern Zaire, *G. c. congöensis*. However, these races have some resemblances both in habitat and pattern and there is the possibility that giraffes from the southern and northern savanna may have been linked at one time, perhaps through a gap in the forests of the Congo basin (see Volume I, pp. 65, 209, 213).

The latitudinal zonation of habitats between the desert and the forest has some correspondence with the distribution of giraffes, for to the north of *G. c. congöensis* there is a distinctive race inhabiting the Sahelian zone. Rock paintings demonstrate that giraffes were once widespread in what is total desert today. Now reduced to a few remnants scattered from Guinea to the Nile, this race, *G. c. peralta*, reaches the borders of the desert in North-east Chad and Kordofan.

Isolated in the eastern Sudan and Eritrea is the typical race *G. c. camelopardalis*, which provides a link between the Sahelian *peralta* and *reticulata* of the Somali arid zone.

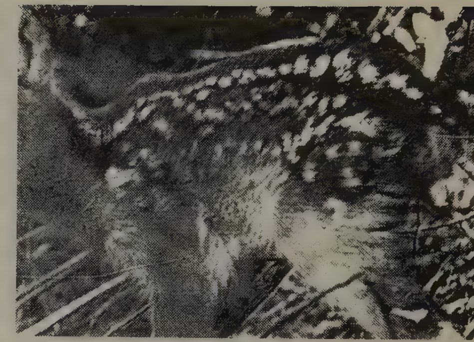
These three populations represent a long west-to-east stepped cline across the drier habitats of northern Africa which curls southwards in Kenya to bring *reticulata* into contact with *tippelskirchi*. The overlap of two extreme ends of a race circle between the Tana and Galana rivers results in a variety of hybrid types in that area with reticulate characteristics generally dominant.

The Uganda and western Kenya *G. c. rothschildi* has a very close affinity with *congöensis* and probably represents an eastern extension of that population. Hybridization with *reticulata* is obvious in Laikipia but genetic mixing may have been extensive in the immediate past because, as I pointed out in Volume I, recent climatic changes have probably allowed giraffes to extend their range in Uganda. The region is situated between three distinct stocks and while *G. c. rothschildi* is predominantly of *congöensis* type, individuals exhibit characteristics of both their other neighbours. These and other representative coat patterns are shown on the colour plate following p. 319, while my interpretation of distribution is summarized on p. 320. The combination of mixing between populations with a large measure of individual variation makes it impossible to describe real "types" but subsequent discussion will attempt to interpret the significance of the very real differences that exist between populations.

Krumbiegel (1939) discussed the evolution of the giraffe's colouring in terms of *G. c. reticulata* representing the "original" type. He considered that a dissolution of pattern could be traced in different races through a process of fragmentation or denting of this regular figure. The question of whether particular pattern elements have evolved through fragmentation or amalgamation is certainly of central relevance to this topic but of all the races *G. c. reticulata* has the most extraordinary pattern and the least like that of any other mammal, and I hope to show how this form might be the product of a process that has passed through a number of distinct phases. While all giraffes possess a highly peculiar type of patterning the progression to which Krumbiegel drew attention suggests to me an evolutionary development in the opposite direction to his. This progression would also accord more closely with the assumption that the giraffe's coat has evolved from the spotty patterns that are widespread among herbivores that rely on crypsis in wooded habitats.

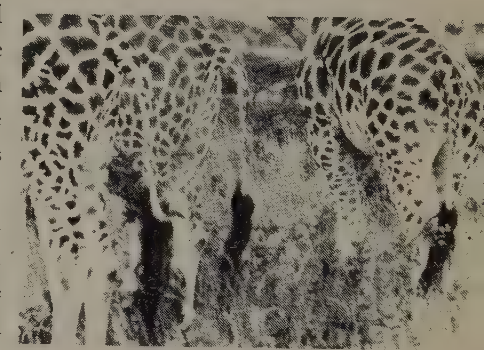
The giraffe today inhabits relatively open woodlands and wooded grasslands but its ecological success depends not only on its great height but also on its size, which is a deterrent to predators. Baby giraffes, instead, recapitulate the species' evolution by passing through a highly vulnerable stage when they remain for long periods of the day lying or standing around on

their own or in "creches". Recent studies have shown that only a quarter of all giraffes born survive the first year of life. The prospects for survival increase with size and in the Nairobi National Park mortality is only 7% in the second year (Foster and Dagg, 1972), illustrating that a giraffe must reach a certain size before it starts to live safely. The ancestral giraffes must also have been shorter, smaller and more vulnerable to predators and if the okapi is anything to go by, their habitat might have been denser than it is today.



Many species of forest dwelling herbivores pass through a cryptically coloured stage while they are young and some retain the pattern into adult life. The resemblances between their blobs and stripes are surprising considering that bovids, deer, chevrotains, pigs, tapirs and some large neotropical rodents must all have evolved these patterns independently.

If the giraffe derived from a smaller forest or woodland dwelling ancestor, the progression towards greater height and drier more open habitats could have put new demands upon the system of camouflage that protected the young. That this might be so can be seen by comparing the tonal configuration in three photographs taken in the wild in typical habitats (opposite). One shows some dappled shadows in woodland surrounding a deer fawn's spotted back, another a small area of bush beside a young giraffe's shoulder.



The fawn's white spots, like those of many other species, are dispersed along a grid over a dark body colour. In evolution, these spot patterns could be easily extended; they can become light horizontal stripes (as in the chevrotain or perhaps the okapi's rump), they can be aligned vertically as on the sitatunga's back, or, by extending in both directions, break up the background into rectangular shapes, as on the flanks of some forest-dwelling bushbuck. In each of these species selection has ensured that stripes are consistently and unequivocally stripes even if individual or local variations in the disposition of pattern suggests that all of them have derived from an elaboration of fawn-like spots. A close examination of individual variation, particularly of the Masai giraffe, *G. c. tippelskirchi*, suggests a similar origin

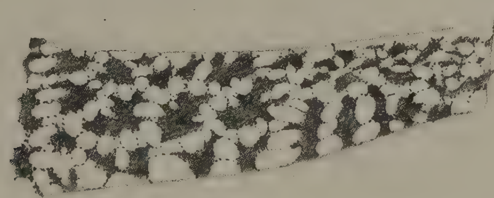


Diagram for comparison with colour plate (T6). (Half-closing the eyes reveals the star-like pattern of dark spots.)

for pattern. In spite of light areas being continuous there are two particulars that suggest that this network might derive from a peculiar ordering of amalgamated spots. If the dark markings on a young Masai giraffe's neck are examined (illustrated in the colour plate), it will be seen that for every concavity there is generally a matching concavity in the dark shape opposite. If these are equated with the edges of irregular light blotches their imaginary outlines can be traced (see diagram) to illustrate how an irregular linear web can be derived from the joining up of very numerous spots.

Ca 1. *G.c. camelopardalis*
Nubian giraffe.

Re 2. *G.c. reticulata*
Reticulated giraffe. Partially amalgamated dark areas. Dark morph (influenced by sex and age.)

Re. 3. *G.c. reticulata*
Reticulated giraffe. Expanded and amalgamated dark areas. Light morph.

P. 4. *G.c. peralta*
West African giraffe.

X. 5. Hybrid *G.c. reticulata* and *G.c. tippelskirchi* from overlap area between Galana and Tana rivers.

T. 6. *G.c. tippelskirchi*
Masai giraffe. Expanded light areas.

T. 9. *G.c. tippelskirchi*
Masai giraffe. Amalgamated dark areas. Dark morph.

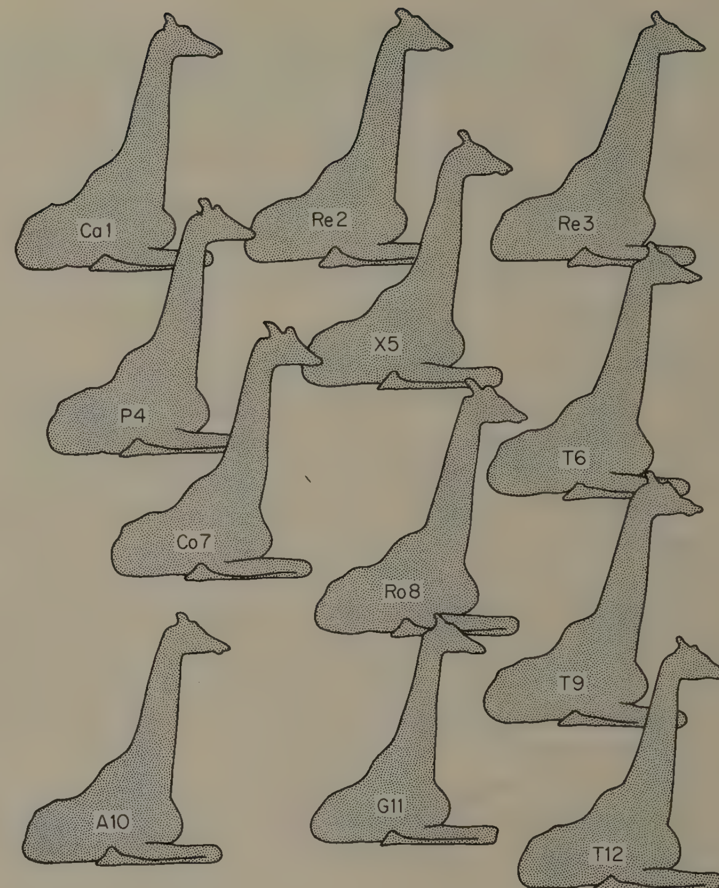
T. 12. *G.c. tippelskirchi*
Masai giraffe. Multiple dark areas.

Co. 7. *G.c. "cottoni"*
Uganda giraffe. Dark morph.

Ro 8. *G.c. rothschildi*
Rothschild's giraffe.

A. 10 *G.c. angolensis*
Angola giraffe.

G. 11 *G.c. giraffa*
Southern giraffe.



The extreme variation from one giraffe to another in the number and spacing of dark figures corresponds with this web. Irregular light lines running in opposite directions demarcate each dark patch and every stage of subdivision is demonstrated. In spite of this the manner of subdivision is consistent. As Krumbiegel (1939) pointed out, the light markings "creep" or erode the dark marks; either fine lines become very numerous or fewer thick lines become thicker still and these variants can be illustrated by examples of coat pattern from two individual Masai giraffes (see plate). The incomplete subdivisions show that the total pattern effect is achieved by a linear extension of lighter areas out into the dark areas but in such a blobby manner as to accord with the idea that they represent an accretion of spots. However, a speciality of the process is that a light mark never appears on its own: light colouring can spread in any direction but only from an established area and it is this combination of random branching together with the consistent absence of any isolated spots that makes the Masai giraffe's jagged pattern rather twig-like.

The numbers and shapes of the islands that are isolated by this branching network of light lines are very variable. Their colour is fairly uniform in *tippelskirchi* but the islands tend to have one or more dark centre-spots in the southern *G. c. giraffa*. The centre-spots tend to expand and darken with age (particularly in old males), and these ontogenetic changes might have a bearing on the evolution in the giraffe's pattern. Differentiating simultaneously out of a neutral or fawn base it would appear that the darker spots simply expand from a scattered and variable number of separate focii whereas the lighter spots link up by "creeping" along irregular but linear pathways.

I think the network pattern is the product of an interaction between these two different spot systems and that genetic control of these systems is sufficiently advanced in all races of living giraffes for light spots never to occur in isolation, while dark spots are always isolated unless they are clustered within a single island of ground colour.

There are wide ranges of variation in the relative proportions of light and dark in every race of giraffe. Apart from an occasional albino, only one wholly unmarked, but otherwise normal, giraffe is known (born in Ueno Zoo, Tokyo). It is light tawny brown all over with pale underparts and it is possible that it is indicative of the base colour on which the spot system operates. It would be particularly interesting to know whether spot formation is controlled by a single gene and whether the Tokyo mutant lacks this gene.

It is interesting that the dark centres of the southern giraffes' pattern have been found to overlie blood vessel complexes or *rete mirabile* just below the skin (Skinner, personal communication).

So far this discussion has concerned the varied patterns of the southern giraffes. The light areas in the northern *peralta* form a broad and relatively even network around well-defined patches of brown. Both tones appear to be more evenly balanced in *peralta* and the breadth of the almost white bands mean that the overall tonal effect is generally lighter in this race than in any other. In spite of individual variation incomplete subdivision of the dark areas is rare. This subdivision was interpreted above as the product of "advances" by the lighter colour into the darker.

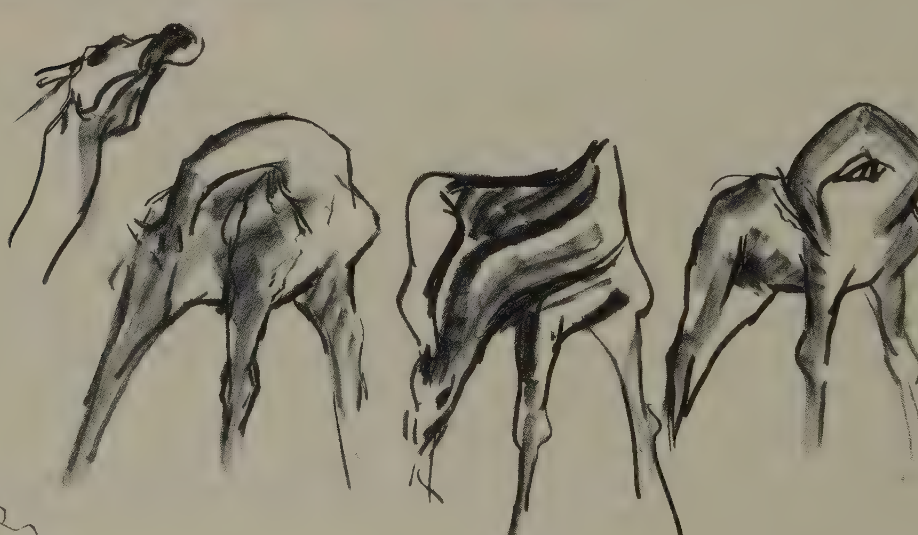
Schema for a hypothetical evolution of giraffe patterns from light and dark foci to star-shapes, patches, and finally, reticulations.

The neutral balance of colours in *peralta* is reversed in *camelopardalis* and *reticulata* in which the number and width of light lines is diminished and there is extensive amalgamation of the dark patches. Because he regarded *reticulata* as the original type, Krumbiegel equated the fine white lines bisecting or quartering its large dark patches with the multitude of eccentric indentations that subdivide the patches in *tippleskirchi*. The fine lines in the former race are more likely to be the last traces of broader ones, product of an overall enlargement and convergence of crisp-edged dark patches. The pattern opposite illustrates this trend.

According to this interpretation the formation of a reticulated pattern would be inconceivable without the development that preceded it. To this extent the giraffes' patterns may be said to follow a progression. Yet each of the four or five major populations is well adapted to its habitat and in practice it would be probably impossible to demonstrate that different patterns influence survival.

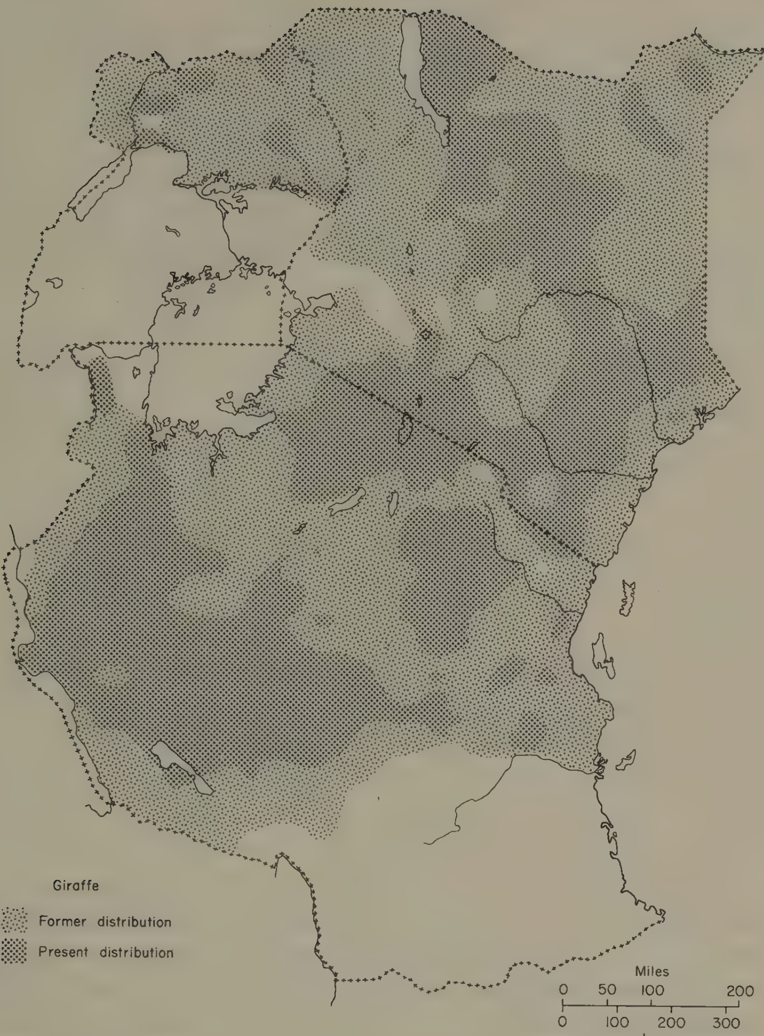
The fact that the lightest coloured race, *peralta*, inhabits the driest, hottest and most open habitats may be significant. Heightened tones would improve thermoregulation in this race but the expansion of white areas has diminished their resemblance to twigs, an effect that probably has less survival value in a thinly treed habitat.

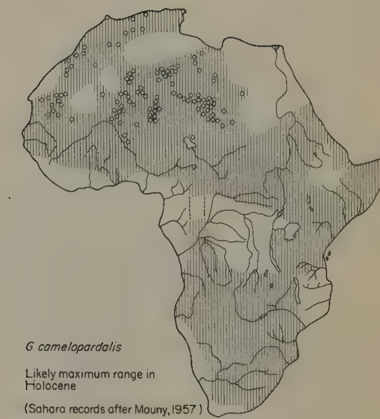
Because the Nubian and reticulated races may have derived from this stock but became isolated in acacia woodland habitats, the expansion of dark areas might represent selection for better camouflage in the more heavily treed environments of north-eastern Africa.



Giraffes were once very widely distributed over many of the savanna areas of the whole continent, but as they are easily killed with traps, arrows, spears and guns their present distribution has been greatly reduced (see maps).

They are commonest in *Acacia*, *Commiphora, Combretum* and open *Terminalia* woodlands. They have always been uncommon in the denser *Brachystegia* woodland and when present tend to spend most of their time on the fringes of drainage lines, where *Acacia* and *Combretum* are common.





Giraffes browse on trees and shrubs of a variety of species but are highly selective. There have been several detailed studies of the giraffe's food and feeding behaviour (Harrison, 1936; Foster, 1966; Wyatt, 1969; Bramachary, 1971a, b; Leuthold and Leuthold, 1972; Moore–Berger, 1974; Hall Martin, 1974a, b). Over 100 species of plants have been recorded in their diet and the choice of plants is determined by local and seasonal availability but the numerous species of Combretaceae and Mimosaceae provide the bulk of their forage. These are often widely dispersed and dominant species, but highly favoured plants may cause giraffes to use pastures or gather in areas that are otherwise unattractive, as when giraffes feed on *Markhamia acuminata* and *Sterculia triphaca* out on open alluvial plains (Harrison, 1936). As the dry season proceeds, the number of trees with green foliage is reduced and giraffes turn to species and habitats that are largely ignored during the rains. For example, Harrison found *Acacia fischeri* and *A. senegal* eaten less in the wet than in the dry season and Hall Martin (1974a) found that riverine evergreens such as *Euclea undulata* and *Maytenus senegalensis*, which account for the bulk of the giraffes' diet at the end of the dry season, are scarcely used at all at other times. Leuthold and Leuthold (1972) found similar patterns in Tsavo.

Fresh foliage is generally preferred and young grass is occasionally taken in small quantities. The fruits of various trees and bushes are also eaten, namely, *Acacia spirocarpa*, *Randia taylori*, *Combretum* spp. *Colophospermum*, *Grewia*, *Strychnos*, *Terminalia* spp. *Sclerocarya*, *Ziziphus*, and in Uganda many giraffes have been shot for eating cotton leaves and bolls in the dry season. Harrison saw groups of giraffe chewing at the bark of *Euphorbia bilocularis* which has an acrid latex and other observers have reported giraffes eating leafless twigs but without specifying plants. Bramachary (1971a, b) noted giraffes at Chobe eating *Combretum binderanum* and *C. gueinzii* but not the more numerous *C. aculeatum*. In this area the main food is the dominant *Harrisonia abyssinica*. Even with the genus *Acacia* some species are avoided, others are eaten rarely and some are visibly more difficult than others to feed on; and Harrison (1936) demonstrated a well-marked pattern of seasonal preferences for the *Acacia* species that were available in Shinyanga.

	Dry season	Wet season
Acacia campylacantha	6	
Acacia drepanolobium		5
Acacia fischeri	12	1
Acacia pennata	1	
Acacia senegal	9	6
Acacia spirocarpa	5	

The more obvious factors influencing the giraffe's preferences are the presence of aromatic substances, the abundance and size of leaves, the shape of thorns, the physical accessibility of a tree and its growth form. They will feed on *A. drepanolobium* on the edges of *mbugas* in the wet season, at which time their hocks may be deep in mud. However, they tend to avoid deeper bogland during the rains, although they will wade quite deep rivers and are reputed to be able to swim.

Twigs of *A. drepanolobium* before and after Giraffe browsing + gall ants

In the Nairobi Park, Wyatt (1969) found that the ant-gall acacia, *A. drepanolobium*, provides the bulk of the giraffe's food throughout the year but he never saw them eating the other common acacia, *A. stuhlmanni*. Giraffes spend relatively little time browsing on an individual tree and the gall-ants, *Crematogaster*, which swarm over their faces might serve to confine their attention to a single branch. It is possible that the long vibrissae around the giraffe's eyelids may help to keep ants out of the eyes as well as anticipate thorns.

Giraffes with their extinct relatives, other browsing ungulates and perhaps chalicotheres, probably influenced the morphology of their principal food trees as they evolved together. Belt (1874) described the special nectaries and galls that provide food and shelter for acacia ants and concluded that these features were adaptations that helped to protect the plant. Brown (1960) has pointed out that acacia species are more numerous in Australia than Africa but only in Africa do they have large browsers to attack them and both thorns and ants to protect them: "the evidence seems to show that where effective browsing mammal faunas are now or recently have been present, the ants have paid their keep." He also considers it possible that the acacia's flat top may be an adaptive response to browsing. The table-topped *A. spirocarpa* is certainly a favourite food but its main photosynthesizing surface is inaccessible to the giraffe.

Giraffes may, therefore, be one of the architects of an African landscape, for not only is there the direct effect of their pruning of trees, particularly *Balanites* and *Ziziphus*, into globular or hour-glass forms, or keeping bushes down to less than a metre, but the shape of numerous species may have evolved to take account of the giraffe and other browsers. Their persistent and heavy browsing of growing acacias often delays the growth of these trees over very extensive areas.

Twigs are pulled into the mouth by the lips and the prehensile tongue which can extend over 450 mm; the twig is raked along its length, which shreds the leaves off and the tip may be cut by the sharp lower incisors. Wyatt found giraffes feeding from head height (6 m) down to the ground, where they eat forbs and fallen fruit.

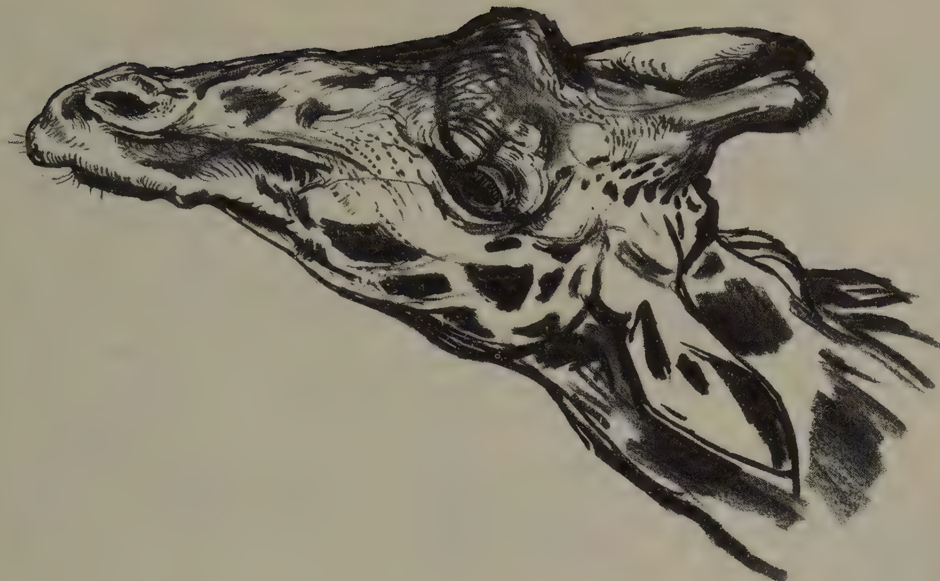
The carcasses of dead animals are often visited by giraffes, which pick up and chew the dried fragments of meat adhering to the bones. The chewing of long bones in this way is perhaps not very different from the chewing of bark off thick branches, which Smithers (1966) suggested is eaten at times of stress.

Feeding continues over sixteen to twenty hours a day and the largest giraffes consume up to 34 kg a day. However, Wyatt (1969) has estimated that a 700 kg giraffe can maintain itself on as little as 7 kg of foliage. Rumination does not require total inactivity and takes up three to five hours in sporadic spells in between feeding. Although capable of surviving without

water for relatively long periods, giraffes visit water and a captive has been recorded drinking 38 litres.

Giraffes orient primarily by sight but their hearing and sense of smell are also acute; they have a sweet musky smell which probably carries well on the wind. For over a hundred years the literature has invariably emphasized the silence of the giraffe. This can be traced back to Owen (1868), who described the vocal apparatus and concluded that the chords were unable to be brought together. In fact, they have a repertoire of sounds not dissimilar to those of some domestic ungulates. Captive calves bellow when they seek their milk and this want call becomes more like a grunt as they get older but is heard in similar situations. All age-classes make loud brays of distress and captive females make roaring bellows after giving birth or when separated from their young. Moaning sounds and short flute-like notes have also been heard.

A mother and her offspring as well as youngsters of similar age form close associations in which there is frequent nuzzling and licking with the muscular lips and tongue. This grooming gesture first associated with sucking may act as a bonding device. Mejia (in Moss, 1976) saw a female nuzzle her young when a hyaena stalked it, which had the effect of inviting a closer approach. The motions derived from grooming may therefore have acquired a communicative function.



The richly haired tassel of the tail is jet black and any movement is very conspicuous. This organ is raised and arched over the back in a tight curl in alarm or flight and is switched whenever the animal is excited.

Male giraffes are very hierarchical and sometimes start reacting to one another from a considerable distance. To this end the postures of the head and neck are peculiarly suited to semaphore information about the status of an individual. For example, submission is indicated by a lowered head and downward ears and a retracted chin puts the head at a sharp angle to the neck. A dominant bull, instead, approaches another with forward stretched head; the neck may be in a lowered or in a vertical "proud" posture but in either case the chin is raised so that the line of the neck runs into the head. In ritualized encounters a dominant male maintains this orientation of the head whatever the position of his neck. Thus in a broadside view the lower part of the neck and shoulders are raised so the neck and head make a taut bow and with a closer approach and challenge the head is thrown up vertically with the horns tilted towards the opponent.

The normal walk of the giraffe is close to a perfect pace with the limbs on one side of the body lifted at approximately the same time. This mode of walking is commonly seen in the gerenuk, the okapi and the camel and is correlated with long legs. A normal gait with alternate legs moving on either side would involve a tiny step for the giraffe or placing of the back leg outside the front (which the giraffe does do when forced to gallop). Apart from the possibility of fore- and back legs interfering with one another, there are important advantages to the pace. The stride can be lengthened and so fewer steps can be taken over a given distance with a resulting economy of energy. The body loses stability but the giraffe's neck provides an ideal counter-balance. After noting the lateral and vertical gyrations of the head and vertebral column, Bourdelle (1934) thought that the giraffe was disproportionately slow for the work involved in maintaining balance. However, the gallop, which does not involve pacing, is actually quite fast (50—60 km per hour). The heavy head moves forward with every power stroke but swings back at the end of each strike in order to keep its balance and counter

the momentum. Thighs bunch up and the lower legs flare out sideways as they come forward almost in synchrony, to be placed outside and well ahead of the foreleg that has taken the animal's weight. The weight-bearing foreleg is always close to the centre of gravity and holding to the midline is probably helped by the extreme narrowness of the thorax between the shoulders (see drawing).

Giraffes can rest standing but prefer to lie with their legs folded beneath them; they rise by splaying their hindlegs and raising their hindquarters. First they get on to their knees and then the head swings up with a jerk as the forelegs straighten in fast succession. While the animal rests it remains alert except for short periods of one to twenty minutes while it sleeps with its head resting on the rump or hindleg.

Feeding is continued intermittently throughout the day but groups may rest and ruminate close together for the hottest part of the afternoon. Activity often continues into the night for some hours and may start well before dawn.

Because their food is generally well dispersed, giraffes too must be widely spaced while feeding and for this reason it is often difficult to know how many animals are in a group, or whether they really constitute a group at all, and Harrison (1936) remarked on their constant breaking up and regrouping. Giraffes are able to accommodate themselves to a wide range of savanna types because each animal can, from a very early age, forage on its own without being tied to another individual. Males exert no restrictions on females and, because the latter are likely to be widely scattered, even in the best of habitats, the male's task of identifying and serving oestrous females seems to have been extended into a continuous perambulation from cow to cow, nuzzling the root of each tail until urine is produced for him to sample. The male's sexual activities, like his food supply, demand continuous travel.

Bull giraffes are great wanderers and they turn up from time to time in areas far from their normal haunts; for example, one such wanderer once got stuck in a drain in Lira, at least 80 km from the nearest known population and, in spite of an average of about 100 people exploring the park every day, Turner (1969) saw a white-necked giraffe near Seronera which had never been recorded before in the Serengeti Park. Female giraffes in the vicinity of Nairobi have an average range of 85 sq km (Foster and Dagg, 1972). Because the males are more difficult to keep track of, these authors could only estimate that ranges must be over 100 sq km. Other evidence of the males' transience emerged from Foster's record of 250 individuals photographed in the course of a three-year study in the Nairobi Park. After a three-year absence, Foster recognized thirty-nine of the adult females but only twenty-nine of the males; he also recorded eleven new adult males to seven new females.

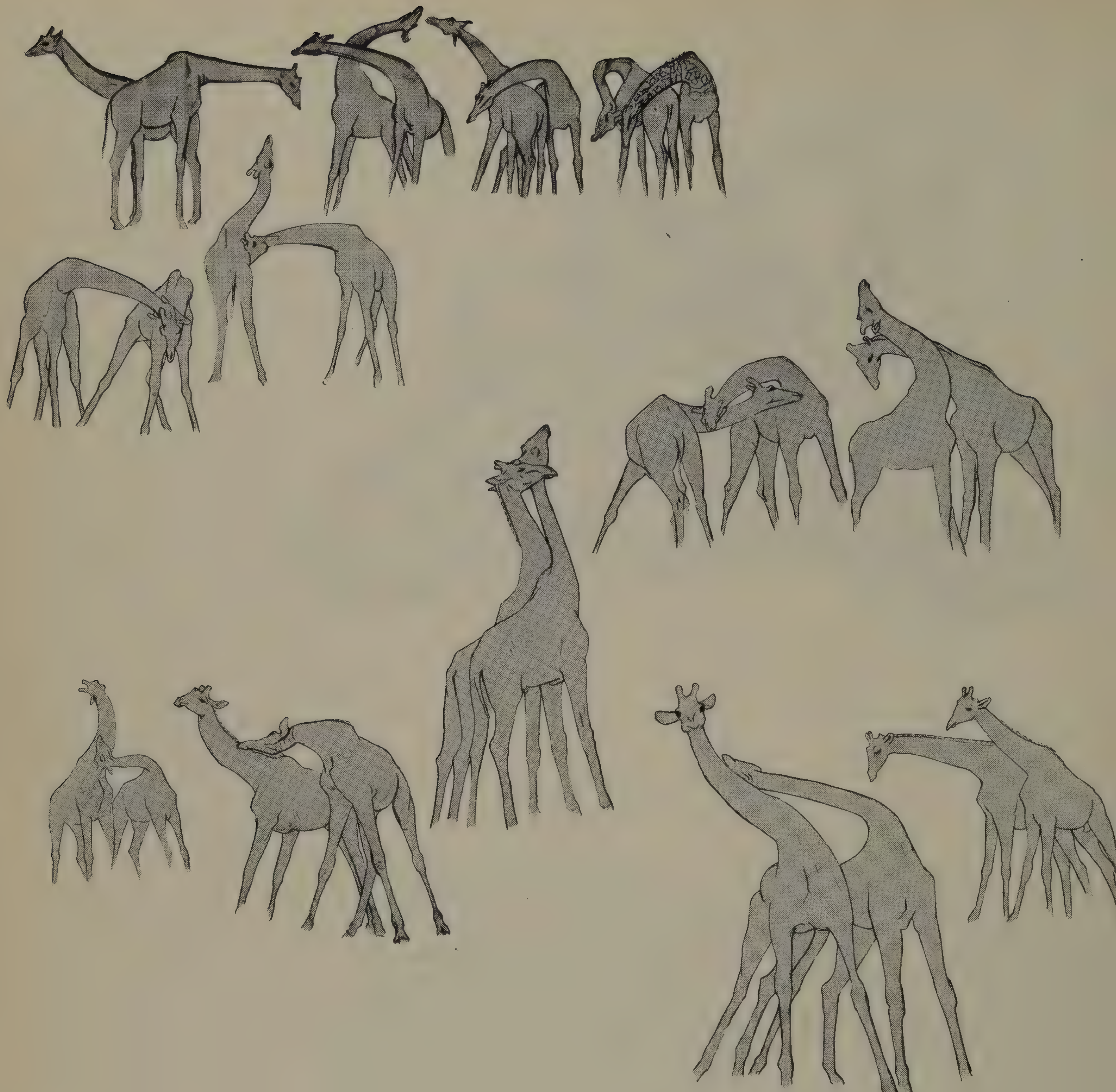
In a restricted area of the Luangwa Valley Barry (1978) estimated that male home ranges averaged about 82 sq km and female, 68 sq km. In Tsavo, Leuthold and Leuthold (1978) estimated an average of 160 sq km, the animals remaining in a relatively small area in the dry season and wandering widely in the rains. At this time male ranges of up to 650 sq km and female ranges of 480 sq km were recorded.

While a male is with a female group, albeit temporarily, he may display herding behaviour and give every sign of being possessive, displaying to and

driving off any other approaching male. Innis (1958) once saw a bull apparently rounding up and herding a group of calves.

In spite of the impermanence of their associations when adult, all giraffes seek company and sociability is so strongly developed in newly born calves that the mother's intolerance of other females at this time may be essential for a proper mother–young bond to develop. As it is, Mejia has found that the bonds between young calves are stronger than with their mothers and as Moss (1976) tells it, Mejia feels that the females only come together because of their calves, implying that the calves may actually facilitate social cohesion in adults. The location of the crèche also provides a focus for the daily movements of the lactating mothers and may therefore be the only important restriction on the females' wanderings. Notwithstanding this, the size of groups tends to vary with the locality rather than with the seasons; 30—50 giraffes commonly browse through acacia woodland, all within sight of one another. Estimates of density made in different localities reflect the browse resources of the area; thus Lamprey (1964) estimated 1·13 per sq km in the well-wooded Tarangire, while Darling (1960), (in the more open Mara National Park) gave 0·27 per sq km. The mixed countryside of the Nairobi Park supports 0·72 per sq km (Foster, 1966).

Several authors have found that more constant companionships are formed among the young than in any other class but this may be a function of their relative immobility; females associate with one another and with their young, but individual ties are very loose. Whenever males associate, whether on their own or in groups of both sexes, the membership is constantly changing. It is uncertain what draws them together into all-male parties but it is in these very temporary groups that a peculiar neck-swinging ritual usually takes place. Typically, one male approaches another with a rather stiff-legged gait and raised nose; turning broadside, the two may circle briefly before coming close together shoulder to shoulder. The animals may face the same or opposite directions but in really vigorous clashes they stand tail to tail. Spreading their legs wide and straining against one another, each contestant arches its neck away from the other before swinging its heavy skull across like a hammer, gaining momentum for a blow with the top of the head. A poorly matched competitor is almost immediately dislodged and retreats from the heavier one, but more evenly matched males can keep up the head clubbing for over half an hour and Smithers (1966) described them going on for hours. The contest is often concluded with the dominant animal mounting the other and a third male has been seen to appear on the scene and proceed to mount both (Moss, 1976). The significance of this behaviour



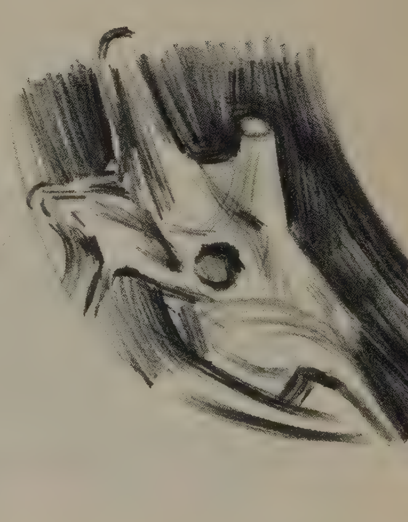
Neck sparring and fighting in male giraffes (traced from photographs).

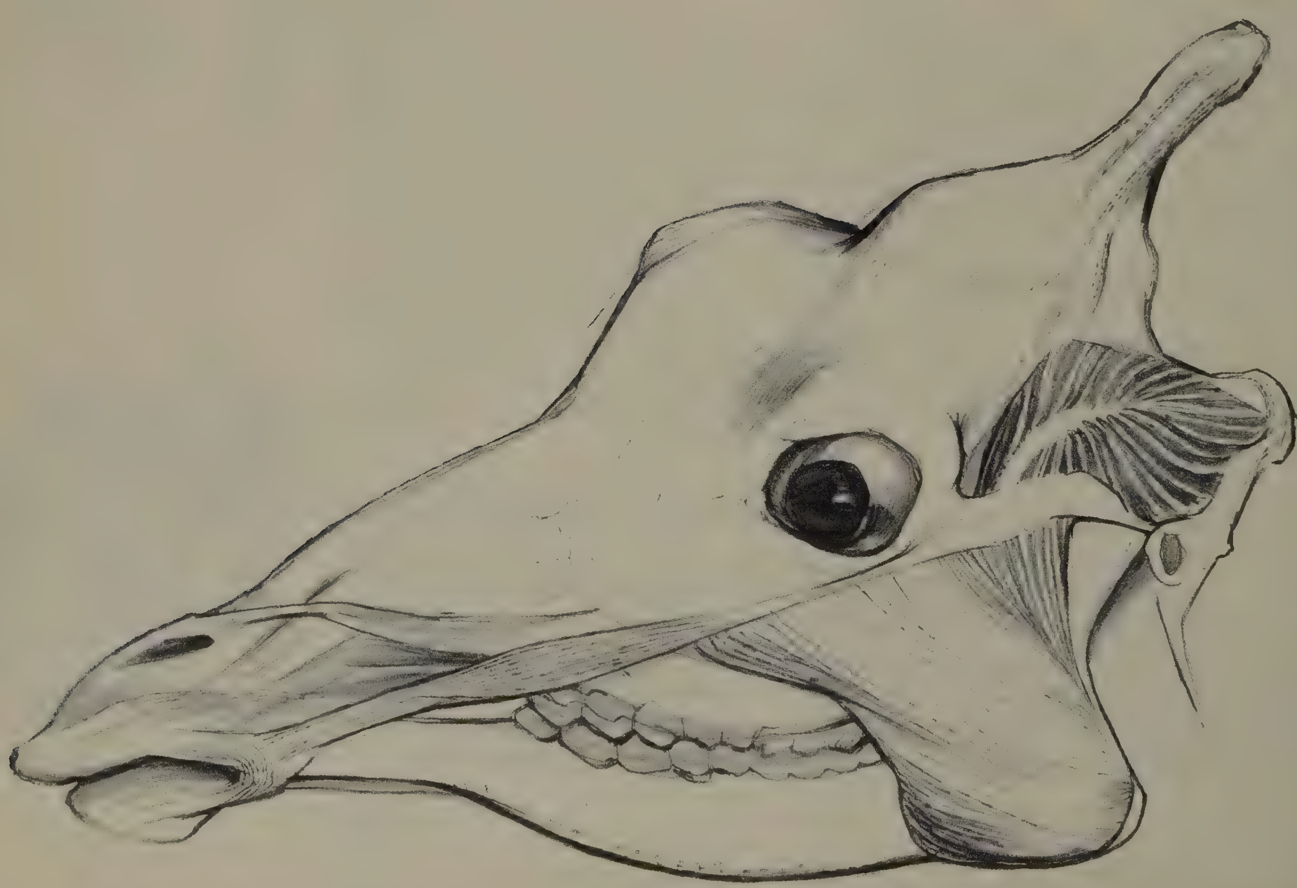
has been discussed by Coe (1967), who pointed out that neck rituals select the most vigorous males without involving serious fights. He stressed that in a society with very impermanent and loose relationships the creation of a dominance hierarchy is most important. The implications of homosexual mountings may have been overstressed by Innis (1958) since this behaviour is a common manifestation of dominance even in female domestic ungulates.

Observers have only seen serious fighting between bulls in the presence of an oestrous female and Downey (pers. comm.) has seen a bull fall unconscious from the concussion of his opponent's blow, then to be hammered with head and hooves while lying prostrate. In the Frankfurt Zoo, an adult bull eland was fatally wounded after being thrown through the air by a blow from the head of a bull giraffe. Backhaus (1961) stated that bulls defend certain cows. In Garamba National Park he watched a bull that had been consorting with a cow break off and indulge in a short but intense fight with another bull. Coe distinguished between the duels of mature bulls attending female groups and temporary bachelor herds indulging in neck rituals. Bachelors are very often immature and even juveniles engage in this activity, which is the equivalent of horn sparring in antelopes and serves to test a young male's strength.

There has been much discussion about sex ratios but there are probably as many males as females in most populations. Horn shapes and skull sizes are subject to astonishing variety particularly in old males, which tend to grow supplementary bony nodules on the upper surfaces of the skull.

Cows coming into oestrus within a mixed group are likely to be monopolized by the largest bull and I have seen such an attendant male drive off another simply by walking towards the intruder in a threatening manner. Mejia saw one bull remain with a cow for three days and he saw one cow avoid mating with other bulls while the first suitor was temporarily absent.





Once the male has discovered signs of oestrus and established his dominance he attends the female very closely. He tries to lay his neck across her back and shoulder and turning his head gently butts her flanks and rump. The female slows down and the male may then walk around her and back into her before mounting. Copulation itself is generally achieved very rapidly.

The gestation period appears to be subject to variation, as does the size of the newborn giraffe. Data from zoo records suggest a range of 427—488 days and a differential of two months is so great that it seems there might be some unknown mechanism for delaying birth. Births are known to occur throughout the year in many localities but there is a widespread tendency for the young to be born in the dry months. A peak has been reported in Serengeti during May and August and in Karamoja between January and March. In Kidepo births are not generally observed after April (Ross, pers. comm.). There may therefore be advantages for the young in being born before the rains and if the differences in gestation periods that have been noted in zoos are real, wild giraffes might have some latitude in the timing of births. (Mejia found that before birth the cow sought out a special calving area.) The mother generally gives birth standing and there are records of wild giraffes dying during labour, with the young jammed with only head and foreleg out. The newborn calf can generally stand after five minutes and will suck within an hour.

Mejia saw mothers behave aggressively towards other females that approached their newborn calves and since young giraffes go through an early stage of investigating anything that moves, this behaviour may serve to ensure that a calf imprints on its mother. At birth the calf is almost 2 metres high and growth is exceptional, averaging nearly three centimetres a day in the first week. At two weeks it will feed on leaves and it seems that a wild calf is capable of being weaned at the age of one month, although in zoos sucking has been observed up to the age of one year.

After the first few days of remaining close to her calf, with frequent contact and suckling, the mother leaves after the early morning suckle to find food, only to return to the creche in the evening. In his Serengeti study area, Mejia found the young calves congregated on woody hilltops while the females browsed in gullies up to 1·5 km away. The sites of crèches evidently vary a lot, for in northern Kenya I have seen a group of unattended young on the middle slopes of a hill covered in acacia scrub and another group was found in northern Tanzania in a small area of *Combretum* savanna in between open flats and riverine thicket.

The calves remain within a small area and although they make no effort to hide themselves they are generally quiet and still, standing and occasionally nibbling at leaves or else lying down, in which case they may form a star-like cluster, all facing out. Mejia found that a calf remains in a crèche for three to four months, after which it begins to accompany its mother but only for a short distance; after feeding for a while it returns to rest up in the crèche. At the age of six months it is moving with the adults and is independent.

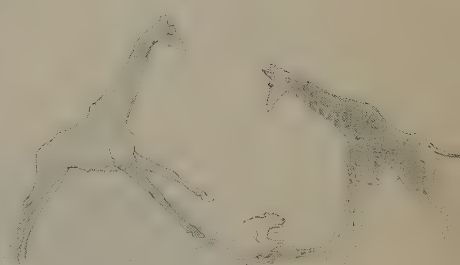
Foster saw one calf leave its mother permanently at the age of two months. Calves are 3 metres high at one year and females become mature before the age of four years, at which time they are 4·5 metres high. Males reach an


on sloping ground

adult size of over 5 metres at seven years. The calving interval is two years unless the calf is lost, in which case conception may be sooner.

The independence and fearlessness of young giraffes renders them an easy prey. Foster and Dagg (1972) estimated a 73% mortality amongst Nairobi Park giraffes during the first year of life and 50% of Serengeti calves are lost in the first three months of life (Mejia in Moss, 1976). Harrison (1936) described lions taking a heavy toll and to this hyaenas and leopards can be added as major predators. Crocodiles have also been recorded killing giraffes. Alternative smaller prey, more numerous and captured with greater ease and less risk, normally shield adult giraffes from predation but considerable numbers were killed by lions in Timbavati Reserve during droughts between 1964 and 1966 (Hirst, 1969b), at which time the lions habitually killed giraffes, which were one of the most numerous ungulates. Schaller (1972) described kills in which rumps and throats had been severely lacerated.

Giraffes have never been seen to kick when fighting. On the other hand, they hit out at predators with their forelegs and Selous watched a mother giraffe drive two leopards away from her calf. Another cow was seen to chase hyaenas off the carcass of a calf that had been killed by lions.



Defensive behaviour; striking out with the forefeet—from photographs

In 1953, a spearman in Lango was run down and killed by a giraffe during a tribal hunt. In most of this area, as in many others, the giraffe has been exterminated in recent years. The principal attraction to poachers is the tail, the hairs of which have been used to thread beads and make necklaces and bracelets since the time of Tutankhamen. To this day giraffe hair bracelets are hawked in the streets of Nairobi and Dar-es-Salaam as good luck charms. Inside and out of the National Parks carcasses have been found with only the tail missing and at one time the Karamojong were reputed to have reconciled their passion for giraffe hair and their respect for government regulations by stalking sleeping giraffes to cut off their brushes. The traditional medicine men of Buganda prescribed smoke of burning giraffe skin as a cure for persistent nose bleeding. The skin is also widely used for sandals and formerly was used for shields.

One of the most commonly depicted animals in the cave paintings of Africa, the giraffe is likely to have been a favourite prey animal for the hunters of the Sahara, of the Kalahari and those of central and eastern Africa. The animal features in the early art of Ancient Egypt and captives were shown in murals of 1500 B.C. Horace and Pliny recorded a giraffe in Rome in 46 B.C. and they reached Rome again in A.D. 247 and 274. In China, a reticulated giraffe was reported to have arrived in 1414 via Arabia and its portrait was painted on silk. Since the early nineteenth century giraffes have been popular animals in European zoos and they have bred in London Zoo since 1836. They will live up to 28 years.

Okapi
(Okapia johnstoni)

Okapi
(Okapia johnstoni)

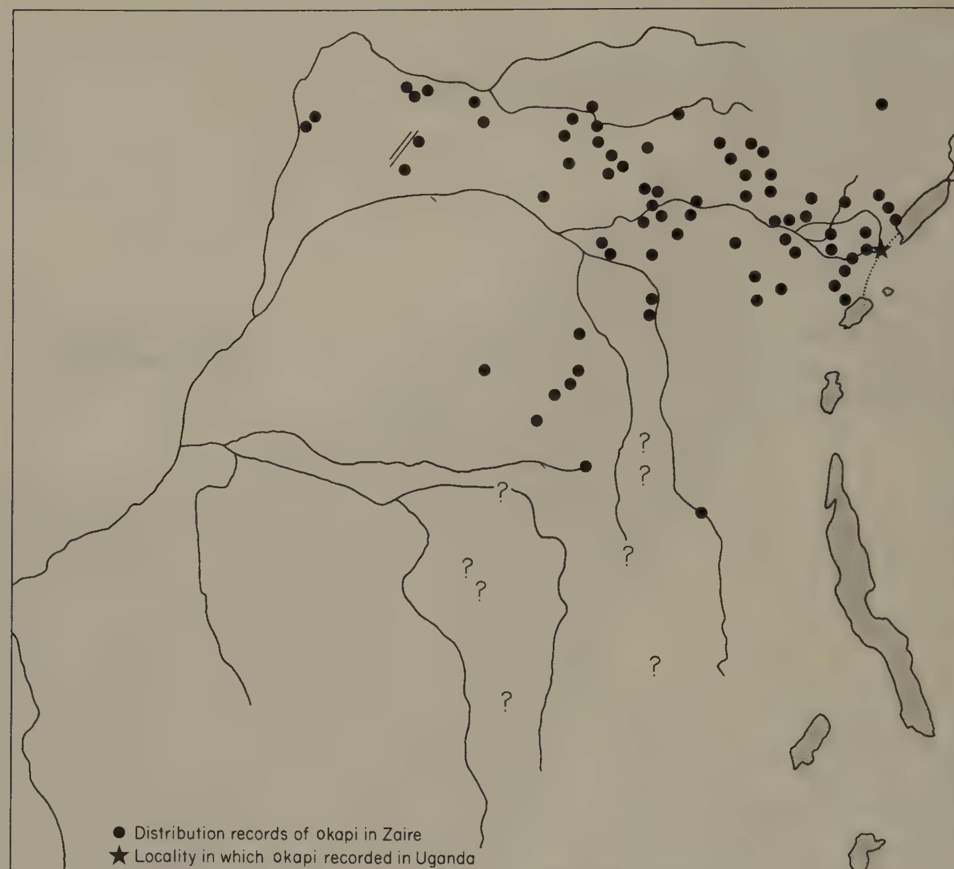
Family	Giraffidae	**Measurements**
Order	Artiodactyla	**head and body**
Local names		210 (197—215) cm
Kenge (Kuamba)		**height**
		150—170 cm
		tail
		30—42 cm
		weight
		210—250 kg

This species is no longer found in Uganda but there is evidence that individuals have wandered into the Semliki Forest Reserve in the immediate past. The principal reservoir of okapi population in the Semliki Valley is some 20 km from the Uganda border and the species is well known to some of the pigmies who commute along the valley. Of two okapis seen in Bwamba around 1953 one was hunted, wounded and lost near the confluence of the Tokwe and Semliki rivers by a hunting party that included one of my pigmy informants. There have been older rumours of okapi in the Kalinzu–Maramagambo forests but these I have been unable to confirm. In Zaire okapis have been recorded in an extensive area between the Ubangi and Semliki rivers and they are thought not to occur much below the 500 m contour.

Okapis are elegant animals and the pigmies' calm assertion to the explorer Stanley that they too had horses like his living wild in the forest is not altogether surprising since their silhouettes are not dissimilar. It was the pigmies' reference to the explorer's horses and mules that led to Sclater's provisional name, *Equus johnstoni*, for his description, which was based on two pieces of zebra-like skin sent to London by Harry Johnston in 1900, ("Okapi" is the name the pigmies gave to the horse so the name has, in a sense, been retained).

Okapis are a rich chocolate-brown with striped hindquarters and legs. The female is redder in colour and slightly larger than the male but she is hornless. The bony spikes above the eyes can sometimes carry a small horn sheath but this is subject to individual variation. Likewise, small vestiges of the fifth metacarpal appear in some individuals (Kock, 1935).

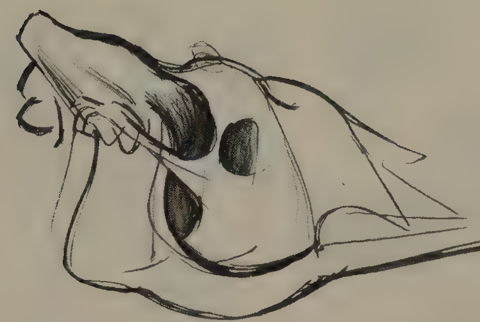
A most strikingly giraffid feature of the okapi is its very long black tongue, with which it plucks buds and leaves or even small branches, by wrapping the muscular prehensile tip around the vegetation and wrenching it into the mouth. The tongue is so long that it can reach the ears and is used for grooming the face as well as the body.

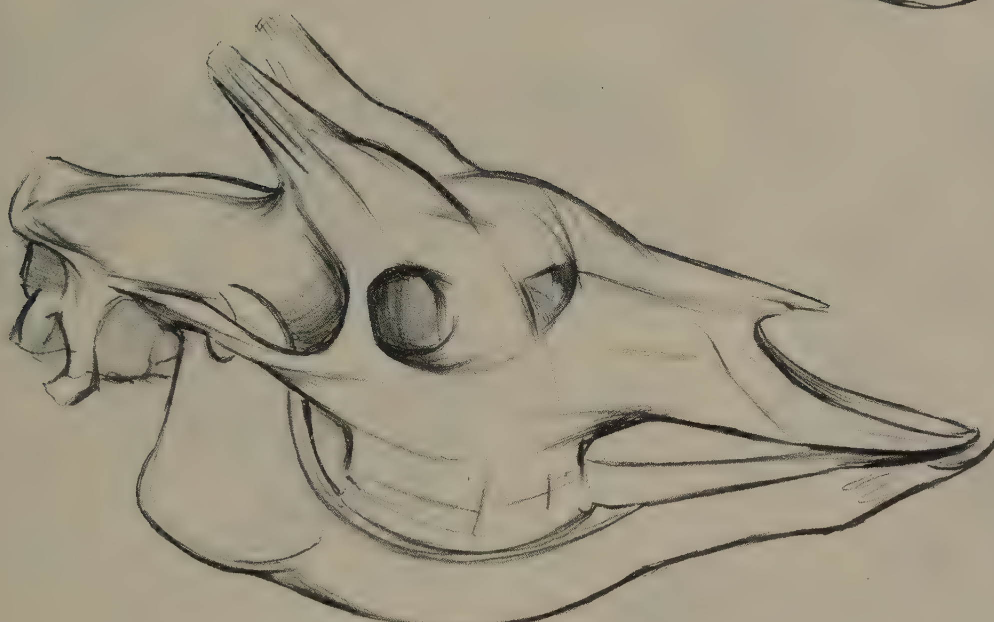


Lists of food plants have been assembled by Ionides (1965) and Landscheere (1957) and include some of the dominant plant species from several distinct forest zones; *Rinorea* spp., the principal forest shrubs, are reported to be their favourite food, also *Drypetes*, which is a short, middle-storey tree growing under a heavy canopy. The leaves of the high canopy trees are of course only available while the tree is young and growing in the undergrowth but many of these species have been recorded. The leaves of *Parinari*, *Alstonia*, *Klainedoxa*, *Khaya*, *Ficus* spp. and *Cynometra* (the climax type in the Semlili Valley, see Volume I, pp. 45–50) have been listed by Ionides. Forest-edge or colonizing species are *Canarium*, *Musanga* and *Spathodea* and the fruits and leaves of the swamp-forest tree, *Mitragyna*, have also been recorded; Ionides also mentions the seeds and young leaves of *Macrolobium*.

Most low level growth is dependent on receiving sunlight, so that clearings and valleys are much frequented by okapis for feeding. The species is generally described as nocturnal but Ionides thought okapis were mainly diurnal. They are reported to shelter under dense cover during storms.

Unlike the giraffe, okapis have pedal glands and Lang (1956) reported wild okapis marking bushes with urine. Bourlière and Verschuren (1960) described the males as nomadic but they follow regular pathways and have favourite areas. The pigmies also assert that they have regular habits and





they catch them in narrow pits dug on these paths. Even when the pits are relatively shallow the animal makes little effort to escape.

There has been no direct observation of wild okapi behaviour and all data on this species come from captive animals. Males have a ritualized neck fight and have been seen to prance about opening the mouth and flaring their nostrils before rushing forward and butting with their horns. Keepers have remarked on the okapi's bad temper when hungry and at Bristol Zoo one female was reported to show consistently an intense interest in visitors dressed in red clothing.

Because okapis are solitary, the periods of courtship and mother–young dependence are the most significant of their social contacts and it is to these aspects of the animal's behaviour that one must look for clues to the meaning of the okapi's extraordinary pattern.

The pattern is peculiar in being entirely confined to the legs and thighs, the stripes occupying panels on the back of the thighs, where they are effectively invisible to their owner. By the same token, the stripes would normally be seen by another animal only if the encounter was at close quarters and friendly, for it is only in such situations that vulnerable parts of the body are exposed.

This disposition of pattern differs fundamentally from that found in the bongo and other bovids, all of which have conspicuous contrasts on their ears, faces and necks, which can be seen from the front. The okapi instead has neutrally coloured ears and neck, dark fronts to the forelegs and a face that lacks contrast when seen head-on (see drawing).

For a calf, its mother's black and white hindquarters must be both a good beacon to follow and a dazzlingly different visual environment while sucking. At this early age the pattern must acquire an overwhelmingly attractive connotation through imprinting, even if there is no in-built genetic response to the pattern, which is also a possibility.

Both motherhood and courtship rely on reinforcement from olfactory, vocal, tactile and visual stimuli. It is known from captives that oestrus lasts over a month, during which time a male will consort closely with a female and wild pairs are thought to behave similarly. The female probably advertises her condition primarily by the scent of her urine and by an oestrus want-call, which would allow the nearest male to track her down. Courtship centres on the genital area and is accompanied by much sniffing, rubbing and circling, interrupted by periods of immobility while they stand side by side, head to tail.

Behaviour sequences often depend upon a barrage of stimuli that condition an animal to make appropriate responses and, in this process, visual elements are often important. While they are circling, each partner must receive a strong visual impact from the moving black and white legs. The less abrupt movements of the hindquarters and even the frequencies of striping are likely to have a qualitatively different effect on the retina but the actual purpose of both pattern elements is likely to be the same, namely, the reinforcement of a temporary but crucial bond in a solitary animal and what might be called a deliberate emphasis on the reproductive function that is the reason for their association.

The tail-view of a female in her oestrous "presenting" posture is truly startling, with radiating white spokes framing her genitalia. However, both sexes are similarly marked and the circling and head-to-tail orientation would normally present an oblique view of the zebra-like rump panel. Seen at close quarters both animals might be dazzled by their partner's zebra-like stripes and, as with these equids, it is conceivable that the optical effect could be an important stimulus and one that is integrated into the animal's behaviour pattern.

In this connexion it may be significant that the white parts of a newborn okapi have longer hair than the dark coloured areas do. This detail may seem insignificant but it could suggest that the width of the dazzling white stripes may be important. Perhaps the tiny proportions of the newborn calf need to be compensated for, so that the white stripes can approximate more closely to the spatial frequency of the adult. Short-term differential growth of hair

is a phenomenon that needs explanation and the most plausible is that it is for visual effect, of which the mother is the only spectator. In the context of the foregoing remarks this could favour the hypothesis that the brain of the solitary okapi might be responsive to a specific frequency range for it to be dazzled into its infrequent but vital partnership with another okapi.

The okapi has bred in zoos and gestation periods range between 427—457 days. Walther (1959) has described the okapi's courtship, which includes several rather antelopine displays, notably head tossing and *laufschlag*.

The young okapi has rather peculiar proportions, having a small head and short neck with thick long legs. It has a well-developed mane that slowly disappears in adults. The young are reported to remain hidden at first and the mother goes to suckle when called. Calves are precocious, walking and sucking within a few hours of birth. Captives have been heard to employ a vocabulary of coughs, bleats and whistles to maintain contact with the mother.

When several mothers and calves are confined together they will suckle one another's young and will hasten to defend any calf. They are weaned by the age of six months and the horns of males may start to develop between the first and the third year. They have lived fifteen years in zoos but are probably capable of living longer.

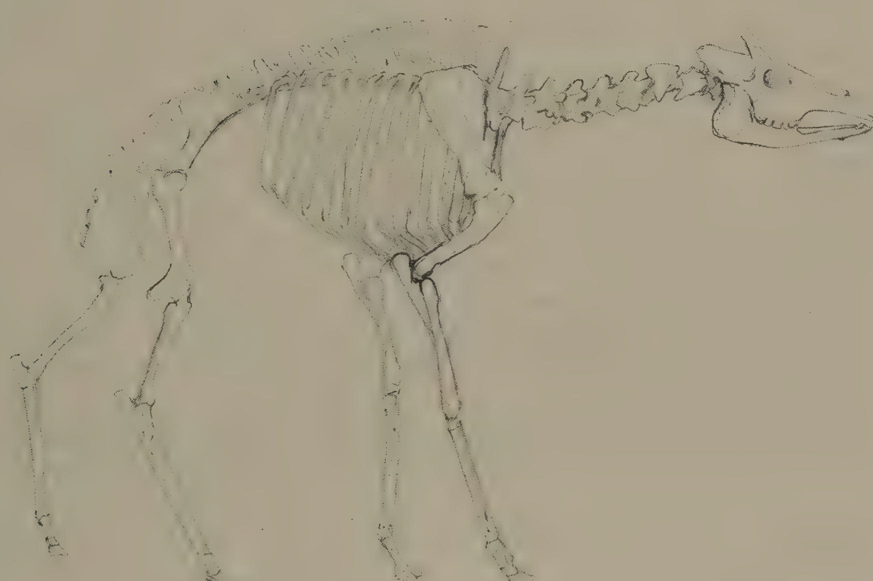
Like giraffes, they use their hooves for attacking, often stamping the ground first with their forefeet before turning round and kicking with the hind ones. A missionary told me of stopping to watch an okapi in the headlights of his car; the animal walked up to the front of the vehicle quite calmly and turning round kicked through the car's radiator.

Leopards are generally regarded to be their major natural enemies. Parasitic infections have been a hazard in captives and among the thirty known parasites, Grzimek (1972) mentions a liver hookworm, *Manodontella*, as being particularly damaging, causing heavy infestation of the bile duct.

The okapi is distributed very locally, as indeed are most large mammals living in forest and estimates of density, which range from 2 to 6 per square mile, take no account of the food and shelter available to the animals; undoubtedly it is relatively common in some localities, notably around Buta and Epulu. In these regions the okapi is still hunted for food and those who have eaten it have assured me of the excellence of its meat.

In Uganda, I was shown a skin which was sold to an ambassador. The Zaire government has made real efforts to maintain the absolute protection this species has enjoyed since 1933 but such traffic is difficult to control.

The chances of a stray okapi surviving in Bwamba Forest today are very slim. The area is now heavily hunted and on my last visit the local game scout was powerless to intervene while aggressive meat hunters were shooting every forest buffalo, elephant, hippo or other large animal they could find and I heard that the situation across the river was little better at that time.



Appendix

Some diseases and parasites recorded from elephants including *Elephas* (from Sikes, 1971).

Anthrax
Foot and Mouth (*Clostridium*)
Rabies
Atheroma
Pleuro-pneumonia
Tuberculosis
Medial sclerosis
Nephritis
Arthritis, rheumatism
Salmonella
Diphtheria
Pasturella

Parasites:
Protozoan *Nuttalia*
Protozoan *Babesia*
Bot flies *Platycobboldia* and *Pharyngobolus*
Warble fly *Ruttenia loxodontis*
Elephant louse *Haematomyzus elephantis*
Ticks (Ixodidae) Amblyomma spp. *Rhipicephalus* spp. *Dermacentor* spp. and *Haemaphysalis*
Roundworms: *Toxocara*, *Leiperenia*, *Murshidia*, *Quilonia*, *Amira*, *Bunostomum*, *Grammocephalus*, *Mammomonogamus*, *Pabronema*.

Flukes:
Brumptia gigas
Fascioloa robustum
Loxodontofilaria

Bibliography

Elephantids and Proboscids

Aguirre, E. (1969a). Evolutionary history of the elephant. *Science, N.Y.* **164**, 1366–1376.

Aguirre, E. (1969b). Revision sistematica de los Elephantidae por su morfologia y morfometria dentaria. *Estudios geologicos* **25**, 123–177; 317–367.

Akeley, C. E. (1912). Elephant hunting in Equatorial Africa with rifle and camera. *Nat. Geogr. Mag.* **23**, 779–810.

Akeley, C. E. (1921). Elephants. *World's Work* **28**, 40–58.

Akeley, C. E. (1929). "Carl Akeley's Africa." (Mary L. Jobe Akeley) Dod Mead and Co., New York.

Allen, G. M. (1936). Zoological results of the G. Vanderbilt African Expedition of 1934. Part II, The forest elephant of Africa. *Proc. Acad. Nat. Sci. Philadelphia* **88**, 15–44.

Ambrosetti, P. (1968). The Pleistocene dwarf elephant of Spinagallo. *Geol. Rom.* **8**, 277–366.

Amoroso, E. C. and Perry, J. S. (1964). The foetal membrane and placenta of the African elephant, *Loxodonta africana*, *Phil. Trans. Roy. Soc. London* **248**, 1–34.

Amoroso, E. C., Franklin, J. J. and Prichard, M. M. L. (1941). Observations on the Cardiovascular system and lungs of an African elephant foetus. *J. Anat.* **76**, 100–111.

Anderson, G. D. and Walker, B. H. (1973). Vegetation composition and elephant damage in the Sengwa Wildlife Research area Rhodesia. *J. S. Afr. Wildl. Mgmt Ass.* 1973.

Andrewartha, H. G. and Birch, L. C. (1954). "The Distribution and Abundance of Animals." University of Chicago Press, U.S.A.

Andrews, C. W. (1904). On the evolution of the Proboscidea. *Phil. Trans. Roy. Soc. London (B)* **196**, 99–118.

Andrews, C. W. (1906). A descriptive catalogue of the Tertiary vertebrata of the Fayum, Egypt, British Museum, London.

Anon., (1966a). Elephant herdleader puts an end to an ailing aged cow. *Afr. Wildlife* **20**, 239–240.

Anon., (1966b). East Africa: the great elephant hunt. *Time* **4**, 39.

Ansell, W. F. H. (1967). Proboscidea. *In* "Preliminary Identification Manual for African Mammals." (Meester, J. ed.), Smithsonian Institution, Washington.

Ansell, W. F. H. (1971). Proboscidea, Perissodactyla, Artiodactyla, *In* "The Mammals of Africa, an Identification Manual". Smithsonian Institution, Washington.

Anthony, R. (1933). Recherches sur les incisives supérieures des Elephantidae actuels et fossiles. *Arch. Mus. Hist. Nat. Paris*, **10** (6), 61–124.

Anthony, R. and Coupin, F. (1925). Nouvelles recherches sur les cavités nasales de l'éléphant d'Asie, *Elephas indicus* L. *Arch. Anat. Hist. Embr.* **4**, 107–147.

Anthony, R. and Friant, M. (1936). Théory de la dentition jugale mammalienne Actualités scient. indust. Paris **372**.

Anthony, R. and Prouteaux, M. (1929). Un crâne d'éléphant d'Afrique. *Loxodonta africana* Blum. à quatre incisives supérieures. *Arch. Mus. Hist. Nat. Paris* **4** (6), 15–31.

Arambourg, C. (1952). Note préliminaire sur quelques éléphants fossiles de Berberie. *Bull. Mus. Hist. Nat. Paris* **2** (24), 407–418.

Arambourg, C., Chavaillon, J. and Coppens, Y. (1969). Résultats de la nouvelle mission de l'Omo. *C.R. Acad. Sci. Paris* **268**, 759–762.

Ayeni, J. S. O. (1974). Some aspects of waterhole utilisation by big game in Tsavo National Park East south of the Voi River. M.Sc. Thesis University of Nairobi.

Babault, G. (1949). Notes on African mammals. *Mammalia* **13**, 1.

Backhaus, D. (1958). Zur Variabilität des ausseren systematischen des afrikanischen Elefanten. *Säugetierk. Mitt.* **6** (4), 173–177.

Badoux, D. M. (1961). A mechanical interpretation of the shape and cyrtocephaly in the skull of the Indian elephant, *Elephas maximus*. *Säugetierk. Mitt.* **9**, 97–105.

Bainbridge, W. R. (1965). Distribution of seed in elephant dung. *Puku* **3**, 173–175.

Baker, S. W. (1863). "Elephant Corps in Uganda." London.

Baker, S. W. (1866). "The Albert Nyanza Great Basin and the Nile." MacMillan, London.

Baker, S. W. (1874). "Ismailia." London.

Baker, S. W. (1890). "Wild Beasts and their Ways: Reminiscences of Europe, Asia, Africa and America." London.

Bakker, R. T. (1971). Dinosaur physiology and the origins of mammals. *Evolution* **25**, 636–658.

Barker, W. (1953). The elephant in the Sudan. *In* "The Elephant in East Central Africa." (C. O. Hill, ed.) Rowland Ward, London and Nairobi.

Bate, D. M. S. (1903). Preliminary note on the discovery of a pigmy elephant in the Pleistocene of Cyprus. *Proc. Roy. Soc. London* 71, 475; 498–500.

Beachey, R. W. (1967). Ivory trade in the 19th century. *J. Afr. Hist.* **8**, 2.

Beadnell, H. J. L. (1905). "The Topography and Geology of the Fayum Province of Egypt." Survey Dept., Cairo.

Beckett, J. (1932). Death of an elephant from rabies. *J. Bombay Nat. Hist. Soc.* **36**, 242–243.

Beddard, F. E. (1893). On the brain of an African elephant. *Proc. Zool. Soc. London* **1893**, 311–315.

Bell, R. H. V. (1969). The use of the herb layer by grazing ungulates in the Serengeti National Park Tanzania. PhD. thesis University of Manchester.

Bell, R. H. V. (1970). The use of the herb layer by grazing ungulates in the Serengeti. *In* "Animal Populations in Relation to their Food Resources." (A. Watson, ed.) Blackwell, Oxford.

Bell, W. D. M. (1923). "The Wanderings of an Elephant Hunter." London.

Bell, W. D. M. (1949). "Karamoja Safari." London.

Bellinge, W. H. S. and Woodley, F. W. (1964). Some notes on rearing of young African elephants. *E. Afr. Wildl. J.* **2**.

Benedict, F. G. (1936). The physiology of the elephant. *Carnegie Inst.* Washington.

Benedict, F. G. and Lee, R. C. (1936). Studies on the body temperature of elephants. *Proc. Nat. Acad. Sci. U.S.A.* **22**, 405–408.

Benedict, F. G. and Lee, R. C. (1938). Further observations on the physiology of the elephant. *J. Mammal.* **19** (2), 175–194.

Benedict, F. G., Fox, E. and Baker, M. (1921). The surface temperature of the elephant, rhinoceros and hippopotamus. *Amer. J. Physiol.* **56**, 464.

Bere, R. (1966). "The African Elephant." Golden Press, New York.

Best, G. A. (Ed.) (1969). "Rowland Ward's Records of Big Game." Rowland Ward, London and Nairobi.

Bishop, W. W. (1958). Miocene mammalia from the Napak volcano, Karamoja, Uganda. *Nature, London* **182**, 1480–1482.

Bishop, W. W. (1963). The later Tertiary and Pleistocene in Eastern Equatorial Africa. *In* "African Ecology and Human Evolution." (Howell, F. C. and Bourlière, F. eds.) Viking Fund Publications in Anthropology No. 36, New York.

Blainville, H. M. D. de (1845). "Ostéographie-Eléphants." Paris.

Blair, P. (1710). The anatomy and osteology of an elephant being an exact description of all the bones of the elephant which died near Dundee 1706 with their several dimensions. *Phil. Trans. Roy. Soc.* **27**, 53–153.

Blancou, L. (1962). A propos des formes naines de l'éléphant d'Afrique. *Mammalia* **26**, 343–361.

Blond, G. (1962). "The Elephants." Andre Deutsch, London.

Blunt, D. E. (1933). "Elephant." London, East Africa.

Boas, J. E. V. and Paulli, S. (1908). "The Elephant's Head." Copenhagen.

Bolton, M. (1973). Notes on the current status and distribution of some large mammals in Ethiopia (excluding Eritrea). *Mammalia* **37** (4), 562–586.

Bourdaire, P. (1897). Domestication de l'éléphant d'Afrique. *C. R. Ass fr. Avan. Sci.*

Bourdelle, E. and Petter, F. (1950). Note relative à un éléphant nain du Gabon. *Mammalia* **14**, 4.

Bourlière, F. (1961). Africa's wildlife in peril. *UNESCO Courier* **9**, 4–7; 34.

Bourlière, F. (1963). Observations on the ecology of some large African mammals. *In* (Howell, F. C. and Bourlière, F. eds.) "African Ecology and Human Evolution." Viking Fund Publications in Anthropology No. 36, New York.

Bourlière, F. (1965). Ecological notes on Tsavo. *Afr. Wildlife* **19** (2), 47–107.

Bourlière, F. and Verschuren, J. (1960). "Introduction à l'écologie des Ongulés du Parc National Albert." Inst. Parcs Nat. Congo Belge, Brussels.

Boyd, J. M. (1966). The changing image of the National Park. *New Scientist* **30**, 254–255.

Brocklesby, D. W. and Campbell, H. (1963). A *Babesia* of the African elephant. *E. Afr. Wildl. J.* **1**.

Brooks, A. C. and Buss, I. O. (1962a). Past and present status of elephants in Uganda. *J. Wildl. Mgmt* **26** (1), 38–50.

Brooks, A. C. and Buss, I. O. (1962b). Trend in tusk size of the Uganda elephant. *Mammalia* **26** (1), 10–34.

Bryden, H. A. (1903). The decline and fall of the South African elephant. *Fortnightly Review* **79**, 100–108.

Buechner, H. K. (1958). Elephant census. Aerial counts of elephants in Murchison Falls National Park and vicinity, Uganda. *Uganda Wildlife and Sport* **1** (4), 17–25.

Buechner, H. K. and Dawkins, H. C. (1961). Vegetation changes induced by elephants and fire in Murchison Falls National Park. *Ecology* **42** (4), 752–766.

Buechner, H. K., Buss, I. O., Longhurst, W. M. and Brooks, A. C. (1963). Numbers and migrations of elephants in Murchison Falls National Park, Uganda. *J. Wildl. Mgmt* **27** (1), 36–53.

Buettner-Janusch, J., Buettner-Janusch, V. and Sale, J. B. (1964). Plasma proteins and haemoglobins of the African elephant and the hyrax. *Nature, London* **201**, 510–511.

Bullock, W. R. (1962). The weight of the African elephant. *Proc. Zool. Soc. London* **138**, 133–135.

Bulpin, T. V. (1962). "The Hunter is Death." London.

Burger, J. F. (1962). Elephant cemeteries. *Field and Tide* **4–5**, 35–36.

Burtt, B. D. R. (1929). Fruit and seed dispersal by mammals in Singida. *J. Ecol.* **17** (2).

Buss, I. O. (1959). Elephant census III. *Uganda Wildlife and Sport* **1**, 25–32.

Buss, I. O. (1961). Some observations on food habits and behaviour of the African elephant. *J. Wildl. Mgmt* **25** (2), 131–148.

Buss, I. O. (1963). Prelude to management—home life of the African elephant. *Animal Kingdom* **66**, 74–79.

Buss, I. O. and Johnson, O. W. (1967). Relationship of Leydig cell characteristics and intratesticular testosterone levels to sexual activity in the African elephant. *Anat. Rec.* **157** (2), 191–196.

Buss, I. O. and Savidge, J. M. (1966). Change in population number and reproductive rate in elephants in Uganda. *J. Wildl. Mgmt* **30** (4), 791–809.

Buss, I. O. and Smith, N. S. (1966). Observations on reproduction and breeding behaviour of the African elephant. *J. Wildl. Mgmt* **30** (2), 375–388.

Buss, I. O. and Wallner, A. (1965). Body temperature of the African elephant. *J. Mammal.* **46** (1), 104–107.

Buss, I. O. and Wing, L. D. (1967). "Elephant use of a tropical rain forest in Uganda." Forest Dept., Uganda.

Butzer, K. W. and Thurber, D. L. (1969). Some late Cenozoic sedimentary formations of the lower Omo basin. *Nature, London* **222**, 1132–1143.

Calder, J. (1975). Elephant killers. *Ill. Lond. News*, June 1975.

Caldwell, K. (1927). Elephant domestication in the Belgian Congo. Report of Game Wardens, Kenya, Uganda 1925. *Reprint. J. Soc. Pres. Fauna Emp.* 71–82.

Carrington, R. (1958). "Elephants." London.

Caughley, G. (1973). The elephant problem—an alternative hypothesis. *E. Afr. Wildl. J.* **14**, 265–283.

Caughley, G. and Goddard, J. (1975). Abundance and distribution of elephants in the Luangwa Valley, Zambia. *E. Afr. Wildl. J.* **13**, 39–48.
Cave, A. J. E. (1959). Pneumatic osteolysis in the elephant skull. *Proc. Zool. Soc. London* **132**, 655–664.
Cave, A. J. E. (1963). Vocal communication in an elephant. *Uganda Wildlife and Sport* 3 (3), 14–19.
Chang, H. (1929). Die Funktion des Kauapparatus bei den Proboscidieren. *Palaeobiol.* **2**, 34–38.
Christie, C. (1924). "Big Game and Pigmies." London.
Clarke, J. M. (1919). An elephant with four tusks. *Science N. Y.* **50**, 395–396.
Cobb, S. (1976). The distribution and abundance of the large herbivore community of Tsavo National Park, Kenya. D.phil. Thesis, Oxford University.
Coe, M. (1972). Defaecation by African elephants, *Loxodonta africana* (Blum.). *E. Afr. Wildl. J.* **10**, 165–174.
Colyer, F. and Miles, A. E. W. (1957). Injuries to and rate of growth of an elephant's tusk. *J. Mammal.* **38**, 243–247.
Cooke, H. B. S. (1947). Variations in the molars of the living African elephant and a critical review of the fossil Proboscidea of Southern Africa. *Amer. J. Sci.* **245**, 434–457; 492–517.
Cooke, H. B. S. (1960). Further revision of the fossil Elephantidae of Southern Africa. *Palaeont. Afr.* **7**, 59–63.
Cooke, H. B. S. (1964). Pleistocene mammal faunas of Africa. *In* "African Ecology and Human Evolution." (Howell, F. C. and Bourlière, F. eds.) Methuen, London.
Cooke, H. B. S. and Coryndon, S. C. (1970). Pleistocene mammals from the Kaiso formation and other related deposits in Uganda. *In* "Fossil Vertebrates of Africa." Vol. 2. (Leakey L. S. B. and Savage, B. J. E. eds.), Academic Press, London and New York.
Cooke, H. B. S. and Maglio, V. J. (1972). Plio-Pleistocene stratigraphy in East Africa in relation to proboscidean and suid evolution. *In* "Calibration of Hominoid evolution." (Bishop, W. W. and Miller, J. A. eds.) Wenner Grenn Symp. pp. 303–329. Scottish Acad. Press.
Coppens, Y. (1965). Les proboscidiens du Tchad. Leur contribution à la chronologie du Quaternaire africain. *Actas V Congres. Panafr. Prehist. Cuaternario 1963* **1**, 331–387.
Coppens, Y. (1972). Un nouveau proboscidien du Pliocène du Tchad, *Stegodibelodon schneideri*, Nov. Gen. Nov. Sp. et le phylum des Stegotetrabelodontinae. *Extrait C. R. Seanc. Acad. Sci.* **1972**, 29 Mai.
Coppens, Y. and Gaudant, M. (1976). Découverte *d'Elephas iolensis* Pomel dans le Tyrrhénien de Tunisie. *Bull. Soc. Géol. Fr.* **1** (7), 171–177.
Corfield, T. F. (1973). Elephant mortality in Tsavo National Park Kenya. *E. Afr. Wildl. J.* **11**, 339–368.
Croze, H. (1972a). The trouble with elephants. *Wildlife News* **7** (2), 2–6.
Croze, H. (1972b). A modified photogrammetric technique for assessing age structures of elephant populations and its use in Kidepo National Park. *E. Afr. Wildl. J.* **10**, 91–115.
Croze, H. (1974). The Seronera bull problem I and II. *E. Afr. Wildl. J.* **12**.
Curry-Lindahl, K. (1967). Congo elephants. *Animals* **9**, 546

Cust, A. M. (1902). "The Ivory Workers of the Middle Ages." London.
Cuvier, G. (1806a). Sur les éléphants vivants et fossiles. *Ann. Mus. Hist. Nat.* **8**.
Cuvier, G. (1806b). Sur le grand mastodonte. *Ann. Mus. Hist. Nat.* **8**.
Cuvier, G. (1817). "Le regne animal I: les pachidermes." Paris.
Cuvier, G. and Laurrilaud, M. (1849). "Anatomie comparée." Paris.
Dart, R. A. (1927). Mammoths and man in the Transvaal. *Nature London* **120** *Suppl.*, 41–48.
Dart, R. A. (1929). Mammoths and other fossil elephants of the Vaal and Lim popo watersheds. *S. Afr. J. Sci.* **26**, 698–731.
Davson, E. (1966). Bark-eating habits by elephants. *Afr. Wildlife* **20**, 1.
Dawkins, H. C. (1961). Vegetation changes induced by elephants and fire in Murchison Falls National Park Uganda. *Ecology* **42**, 752–766.
Debeer, G. R. (1955). "Alps and Elephants: Hannibal's march." Geoffrey Bles, London.
Deraniyagala, P. E. P. (1955). "Some extinct elephants their relatives and the two living species." Ceylon Nat. Mus. Pub., Columbo.
Deraniyagala, P. E. P. (1968). Three extinct mammals from Africa. *J. Palaeont. Soc. India* (5–9), 16–20.
Dietrich, W. O. (1943). Über innerafrikanische Mastodonten. *Z. Dt. Geol. Ges.* **95**, 46–48.
Dietrich, W. O. (1951). Daten zu den fossilen Elefanten Afrikas und Ursprung der Gattung *Loxodonta*. *Neues Jhrb. Geol. Pal. Abhandl.* B **93**, 325–378.
Dittrich, L. (1967). Beitrag zur Fortpflanzung u. Jugendentwicklung des indischen Elefanten in Gefangenschaft. *Zool. Gart. (NF) Leipzig* **34**, 56–92.
Dittrich, L. (1974). Ersatz des Milchschneidezahnes durch den Stosszahn beim Indischen Elefanten, *Elephas maximus*. *Z Säugetierk.* **39**, 58–64.
Dollman, G. (1931). Four-tusked elephants. *Proc. Linn. Soc. London* **143**, 74–78.
Dollman, G. (1934). Pigmy elephants. *Nat. Hist. Mag.* **4**, 266–271. (Trustees of the British Museum, London.)
Doremus, C. A. (1882). Analysis of an elephant's milk. *Med. News N. Y.* **40**, 282.
Dougall, H. W. (1936). On the chemical composition of elephant faeces. Research notes. *E. Afr. Wildl. J.* **1**.
Dougall, H. W. and Sheldrick, D. L. W. (1964). The chemical composition of a day's diet of an African elephant. *E. Afr. Wildl. J.* **2**, 51–59.
Douglas-Hamilton, I. (1972). (1973). (1975). See Hamilton.
Driak, F. (1933). Anatomical and histological examination of the structure and development of the elephant molar. *J. Dent. Res.* **13**, 213.
Drummond, W. H. (1875). "The Large Game and Natural History of South and South-East Africa."
Duncan, W. R. H. and Garton, G. A. (1968). The fatty acid composition and intramolecular structure of triglycerides from adipose tissue of the hippopotamus and the African elephant. *Comp. Biochem. Physiol.* **25**, 319–325.

Eales, N. B. (1926). The anatomy of the head of a foetal African elephant, *Loxodonta africana. Trans. Roy. Soc. Edinburgh* **54**, 491–551.

Eales, N. B. (1928). Anatomy of a foetal African elephant, part II. *Trans. Roy. Soc. Edinburgh* **55**, 203–246.

Eales, N. B. (1929). The anatomy of a foetal African elephant, part III. *Trans. Roy. Soc. Edinburgh* **56**, 203–246.

Elder, W. H. and Rodgers, D. H. (1968). Age and growth of elephants. *Afr. Wildlife* **22**, 281–293.

Eltringham, S. K. and Malpas, R. C. (1976). Elephant slaughter in Uganda. *Oryx* **13** (4).

Eltringham *et al.* (1974). See Wyatt.

Elwes, H. G. (1915). Altitude to which elephants ascend. *J. Bombay Nat. Hist.* **24**, 355 (1915–1917).

Evans, G. M. (1910). "Elephants and their Diseases: A treatise on elephants." Rangoon.

Falconer, H. and Cautley, P. T. (1845–1849). "Fauna antiqua Sivalensis. Being the fossil zoology of the Sewalik Hills in the north of India." Smith Elder and Co., London.

Falconer, T. (1797). "The Voyage of Hanno." T. Calder Junior & Davies, London.

Ferrier, A. J. (1948). "The Care and Management of Elephants in Burma." London.

Field, C. R. (1971). Elephant ecology in the Queen Elizabeth National Park Uganda. *E. Afr. Wildl. J.* **9**, 123.

Field, C. R. and Ross, I. C. (1976). The savanna ecology of the Kidepo Valley National Park II. Feeding ecology of elephant and giraffe. *E. Afr. Wildl. J.* **14** (1), 1–15.

Flower, S. (1947). Further notes on the duration of life in mammals. V: The alleged and actual ages to which elephants live. *Proc. Zool. Soc. London* **117**, 680–688.

Foran, W. R. (1958a). Ivory's decline in Africa. *Field, London* **212**, 368.

Foran, W. R. (1958b). Elephants killed by a mouse. Letter to *Field, London* **212**, 372.

Forbes, W. A. (1879). On the anatomy of the African elephant (*Elephas africanus* Blum.). *Proc. Zool. Soc. London* **1879**, 420–435.

Ford, J. (1966). The role of elephants in controlling the distribution of tsetse flies. *IUCN Bull.* **19** (6).

Fosbrooke, H. A. (1968). Elephants in Serengeti: an early record. *E. Afr. Wildl. J.* **6**, 150–152.

Foster, J. B. and Coe, M. J. (1968). The biomass of game animals in Nairobi National Park 1960–66. *J. Zool. London* **155**, 413–425.

Frade, F. (1931). Sur l'existence en Afrique de deux espèces d'éléphants. *Bull. Soc. Portugaise des Sci. Nat.* **XI**, 9, 1931.

Frade, F. (1933). Eléphants du Mozambique. *Bull. Soc. Port. Sci. Nat.* **11**, 307–318.

Frade, F. (1933). Eléphants d'Angola. *Bull. Soc. Port. Sci. Nat.* **11**, 319–333.

Frade, F. (1936). Distribution géographique des éléphants d'Afrique. *C.R. XII. Congr. Internat. Zool. Lisbonne.*
Frade, F. (1955). Order des Proboscidiens. *In* "Traité de Zoologie." Vol. 17 Mammifères Systématique (Grassé, P. P., ed.), Masson et Cie, Paris.
Gaudry, A. (1878). Les enchaînements du monde animal dans les temps géologiques. "Mammifères tertiaires." Paris.
Giard, A. (1907a). A quel moment et comment s'oblitèrent les cavités pleurales des éléphants? *C. R. Hebd. Séanc. Acad. Sci. Paris* **144**.
Giard, A. (1907b). L'éléphant d'Afrique a-t-il une cavité pleurale? *C. R. Hebd. Séanc. Acad. Sci. Paris* **144**.
Gilett, G. K. (1965). Elephant behaviour. *Afr. Wildlife* **19**, 339.
Gingrich, P. D. (1971). Functional significance of mandibular translation in vertebrate jaw mechanics. *Postilla* **152**, 1–10.
Glover, J. (1963). The elephant problem at Tsavo. *E. Afr. Wildl. J.* **1**, 30–39.
Glover, P. E. and Sheldrick, D. (1964). An urgent research problem on the elephant and rhino populations of the Tsavo National Park Kenya. *Bull. Epizoot. Dis. Afr.* **12**, 33–38.
Gordon, C. G. (1881). "Colonel Gordon in Central Africa 1874–1879." (Hill, G. B. ed.), De la Rue, London.
Gordon, J. A. (1966a). Elephants do think. *Afr. Wildlife J.* **1**, 30–39.
Gordon, J. A. (1966b). *Loxodonta* dig hole for water and then plug it. *Afr. Wildlife* **20**.
Gough, (1973). (In Guy, 1974).
Gowers, W. (1948). African elephants and ancient authors. *African Affairs, London*, **47**, 173–180.
Gowers, W. (1953). The african elephant in history. *In* "The Elephant in Central Africa." Rowland Ward, London and Nairobi.
Gregory, W. K. (1903). Adaptive significance of the shortening of the elephant's skull. *Bull. Amer. Mus. Nat. Hist.* **19**, 387–394.
Gromier, E. (1907). Protection et utilisation de l'éléphant d'Afrique. *Bull. Soc. Géogr. Lyon* **22**.
Grzimek, B. (1956). Ein merkwurdiges Verhalten von Afrikanischen Elefanten. *Z. Tierpsychol.* **13**, 151–152.
Gulliver, G. (1847). Note on the spermatozoa and on the elevator muscles of the penis of the Indian elephant. *Proc. Zool. Soc. London* **1847**.
Guy, P. R. (1974). Feeding behaviour of the African elephant in Sengwa Research area of Rhodesia. MSc. thesis University of Rhodesia.
Hamilton, A. C. (1972). The interpretation of pollen diagrams from highland Uganda. *Palaeoecology of Africa* **7**, 45–149.
Hamilton, A. C. (1974a). Distribution patterns of forest trees in Uganda and their historical significance. *Vegetatio* **29**, 21–35.
Hamilton, A. C. (1974b). The history of the vegetation of East Africa. *In* "East African Vegetation." (Lind, E. M. and Morrison, M. E. S. eds.), pp. 188–209. Longman, London.
Hamilton, A. C. (1976). The significance of patterns of distribution shown by forest plants and animals in tropical Africa for the reconstruction of upper Pleistocene palaeoenvironments: a review. Reprint from "Palaeoecology of Africa, the Surrounding Islands and Antarctica." (van Zinderen Bakker, E. M. ed.) Vol. IX Balkema Cape Town.

Hamilton, I. (1972). On the ecology and behaviour of the African elephant. D. Phil. thesis University of Oxford.
Hamilton, I. (1973). On the ecology and behaviour of the Lake Manyara elephants. *E. Afr. Wildl. J.* **11**, 401–403.
Hamilton, I. and Hamilton, O. (1975). "Among the Elephants." Collins, London.
Hammond, K. (1978). Ivory from Zaire. *New Scientist* Vol. 78, No. 1099.
Hanks, J. (1969a). Growth and weight of the female African elephant in Zambia. *E. Afr. Wildl. J.* **7**, 7–10.
Hanks, J. (1969b). Seasonal breeding of the African elephant in Zambia. *E. Afr. Wildl. J.* **7**, 167.
Hanks, J. (1969c). Elephants know best. *Black Lechwe* **7** (5), 12–15.
Hanks, J. (1971). The elephant problem. *World Wildlife Yearbook* 1970–71.
Hanks, J. (1972a). Reproductive physiology of *Loxodonta africana*. PhD. thesis, University of Cambridge.
Hanks, J. (1972b). Growth of the African elephant, *Loxodonta africana*. *E. Afr. Wildl. J.* **10** (4), 251–272.
Hanks, J. (1972c). Growth of the Asian and African elephant, Elephas maximus and *Loxodonta africana*. *Quart. Rev. Biol.* **1972**.
Hanks, J. (1972d). Aspects of dentition of the African elephant *Loxodonta africana*. *Arnoldia Rhodesia* **5** (36), 1–18.
Hanks, J. (1973). Reproduction of the female African elephant in the Luangwa Valley Zambia. *J. S. Afr. Wildl. Mgmt Ass.* **3** (2) 1973.
Hanks, J. and McIntosh, J. E. A. (1973). Population dynamics of the African elephant *Loxodonta africana*. *J. Zool. London* **169**, 29–38.
Hanks, J. and Short, R. V. (1972). The formation and function of the *corpus luteum* of the African elephant *Loxodonta africana*. *J. Reprod. Fert.* **1972**.
Hardwick, A. S. (1903). "An Ivory Hunter in North Kenya." London.
Harris, L. D. (1968). Population dynamics of the African elephant in the Mkomazi Game Reserve Tanzania. MSc. thesis Michigan University, East Lansing.
Harthoorn, A. M. (1966). The Tsavo elephants. *Oryx* **8** (4), 233–236.
Harthoorn, A. M. (1970). "The Flying Syringe." Geoffrey Bles, London.
Haughton, S. H. (1932). On some South African fossil Proboscidea. *Trans. Roy. Soc. S. Afr.* **21**, 1–18.
Heath, B. R. and Field, C. R. (1974). Elephant endurance on Galana Ranch Kenya. *E. Afr. Wildl. J.* **12**, 239–242.
Hendrichs, H. and Hendrichs, U. (1971). "Dik-dik und Elefanten." Verlag Piper, Munich.
Henshaw, J. (1972). Notes on conflict between elephants and some bovids and other inter-specific contacts in Yankari Game Reserve N. E. Nigeria. *E. Afr. Wildl. J.* **10**, 151–153.
Hill, W. C. O. (1953). The evolution of the African Elephant *and* The reproduction of the African elephant. *In* "The Elephant in East Africa." Rowland Ward, London and Nairobi.
Hillaby, J. (1961). Elephants as pest control problem. *New Scientist* **12**, 736–738.
Holder, C. F. (1886). "The Ivory King: a popular history of the elephant and its allies." London.

Holloway, C. W. (1965). Big game in Kenya Forests. *Commonw. For. Rev.* **44** (2), 120.
Holman, D. (1967). "The Elephant People." John Murray, London.
Hooijer, D. A. (1949). Pleistocene vertebrates from Celebes IV *Archidiskodon celebensis*. *Nov. Sp. Zool. Med. Mus. Leiden* **30** (14), 205–226.
Hooijer, D. A. (1954). A pigmy *Stogodon* from the Middle Pleistocene of Eastern Java. *Zool. Med. Mus. Leiden* **33** (14), 91–102.
Hooijer, D. A. (1955). Fossil Proboscidea from the Malay Archipelago and the Punjab. *Zool. Verband Mus. Leiden* **28**, 1–146.
Howell, F. C. (1968). Omo Research Expedition. *Nature, London* **219**, 567–572.
Hubbard, W. D. (1928) Observations on the elephant of northern Rhodesia and Portuguese East Africa. *J. Mammal.* **9**, 39–43.
Hundley, G. (1922). The breeding of elephants in captivity. *J. Bombay Nat. Hist. Soc.* **28**, 537–539.
Hutchinson, A. (1975). Elephant survival—two schools of thought. *Wildlife Mag.* **17** (3), 104–107.
Irwin, T. E. (1963). Elephants' stomach rumbles. *Afr. Wildlife* **17** (2), 112.
Irwin, T. E. (1964) Large tuskers in Tanganyika. *Afr. Wildlife* **18**, 229–234.
Jacobi, E. F. (1967). Olifanten aan het werk. *Artis. Amst.* **13**.
Jainudeen, M. R., Katongole, C. B. and Short, R. V. (1972a) Plasma testosterone levels in relation to musth and sexual activity in the male Asiatic elephant. *J. Reprod. Fert.* **29**, 99–103.
Jainudeen, M. R., McKay, G. M. and Eisenberg, J. F. (1972b). Observations on musth in the domesticated Asiatic elephant. *Elephas maximus. Mammalia* **36** (2), 247–262.
Jeannin, A. (1947). "L'éléphant d'Afrique: zoologie, histoire, folklore, chasse, protection." Payot, Paris.
Johnson, O. W. (1964). Histological and quantitative characteristics of the testes, observations on the teeth and pituitary gland and the possibility of reproductive cyclicity in the African elephant. *Diss. Abstr.* **25**, 1422.
Johnson, O. W. and Buss, I. O. (1965). Molariform teeth of the male elephant in relation to age, body dimensions and growth. *J. Mammal.* **46** (3), 373–384.
Jordan, J. A. (1956). "Elephants and Ivory." New York, London.
Keynes, Q. (1951). Africa's uncaged elephants. *Nat. Geogr. Mag. Washington*, (March).
Kortlandt, A. (1976). Tree destruction by elephants in Tsavo National Park and the role of man in African ecosystems. *Netherl. J. Zool.* **26** (3).
Krumbiegel, I. (1943). Der Afrikanische Elefant. *Monogr. Wildsäugetiere Lpz.* **9**, 1–152.
Krumrey, W. A. and Buss, I. O. (1968). Age estimation growth and relationships between body dimensions of the female African elephant. *J. Mammal.* **49**, 22–31.
Kühme, W. (1960). Die Afrikanische Elefanten des Georg-von-Opel-Freigeheges. *Yb. G. v. Opel-Freigeheges* 3, 17–29.
Kühme, W. (1961). Beobachtungen am afrikanischer Elefanten in Gefangenschaft. *Tierpsychol.* **18**, 285–296.

Kühme, W. (1962). Erganzenden Beobachtungen an afrikanischen Elefanten in Freigehege. *Sonderdruck aus Z. Tierpsychol.* **20** (1), 66–79.
Kühme, W. (1963). Ethology of the African elephant *Loxodonta africana*. Blum. in captivity. *Int. Zoo Yearbook* **4**, 113–121.
Kunz, G. F. (1916). "Ivory and the Elephant in Art, in Archaeology and in Science." New York.
Kurt, F. (1960). Le sommeil des éléphants. *Mammalia* **24**, 258–272.
Kurt, F. (1974). Remarks on the social structure and ecology of the Ceylon elephant in the Yala National Park. *In* "The Behaviour of Ungulates and its Relation to Management. (Geist V. and Walther, F. eds.), IUCN Pub. 24.
Kurten, B. (1968). "Pleistocene Mammals of Europe." Weidenfeld and Nicholson, London.
Lamprey, H. F. (1963). Ecological separation of the large mammal species in the Tarangire Game Reserve Tanganyika. *E. Afr. Wildl. J.* **1**, 63–92.
Lamprey, H. F., Glover, P. E., Turner, M. I. M. and Bell, R. H. V. (1967). Invasion of the Serengeti National Park by elephants *E. Afr. Wildl. J.* **5**, 151–161.
Lang, E. M. (1965). Zahnbeobachtungen bei Elefanten. *Z. Saugetierk.* **30**, 287–297.
Lang, E. M. (1967). The birth of an African elephant *Loxodonta africana* at Basle Zoo. *Int. Zoo. Yearbook* **7**, 154–157.
Laws, R. M. (1966). Age criteria for the African elephant *Loxodonta africana. E. Afr. Wildl. J.* **4**, 1–37.
Laws, R. M. (1967a). Occurrence of placental scars in uterus of the African elephant *Loxodonta africana. J. Reprod. Fert.* **14**, 445–449.
Laws, R. M. (1967b). Eye lens weight and age in African elephants. *E. Afr. Wildl. J.* **5**, 46–52.
Laws, R. M. (1968a). Preliminary report on 300 elephants culled in the Mkomazi Game Reserve in March–April 1968 Tanzania. (Govmt. Typescript.)
Laws, R. M. (1968b). Interactions between elephant and hippopotamus populations and their environments. *E. Afr. Agric. For. J.* 33 (special issue) 140–147.
Laws, R. M. (1969a). Aspects of reproduction in the African elephant *Loxodonta africana. J. Reprod. Fert. Suppl.* **6**, 193–217.
Laws, R. M. (1969b). The Tsavo Research Project. *J. Reprod. Fert. Suppl.* **6**, 495–531.
Laws, R. M. (1970a). Elephants as agents of habitat and landscape changes in East Africa. *Oikos* **21**, 1–15.
Laws, R. M. (1970b). Biology of African elephants. *Science Progress Oxf.* **58**, 251–262.
Laws, R. M. (1974). Behaviour dynamics and management of elephant populations. *In* "The Behaviour of Ungulates and its Relation to Management. (Geist, V. and Walther, F. eds.), IUCN Publ. 24.
Laws, R. M. and Parker, I. C. S. (1968). Recent studies on African elephant populations in East Africa. *In* "Comparative Nutrition of Wild Animals." (Crawford, M. A. ed.) pp. 319–359. Symp. Zool. Soc. No. 21. Academic Press, London and New York.

Laws, R. M., Parker, I. C. S. and Archer, A. L. (1967). Estimating live weights of elephants from hindleg weights. *E. Afr. Wildl. J.* **5**, 106–111.
Laws, R. M., Parker, I. C. S. and Johnstone, R. C. B. (1970). Elephants and habitats in North Bunyoro Uganda. *E. Afr. Wildl. J.* **8**, 163–180.
Laws, R. M., Parker, I. S. C. and Johnstone, R. C. B. (1971). Elephants and their habitats. The status of elephants in North Bunyoro Uganda. *E. Afr. Wildl. J.* **8**, 163–180.
Laws, R. M., Parker, I. S. C. and Johnstone, R. C. B. (1975). "Elephants and their Habitats." Clarendon Press, Oxford.
Lenkeit, W. (1933). Time required for food to pass through the digestive tract of domestic animals. *Ergebn. Physiol.* **35**, 573.
Leuthold, W. (1973). Recent elephant counts in Tsavo National Park. Report to the Trustees of Kenya National Parks. (Mimeo) 17 pp.
Leuthold, W. (1975). Studies on the age structure of the Tsavo elephant population with special reference to the 1970–71 mortality. (Mimeo) 9 pp.
Leuthold, W. (1976). Group size in elephants of Tsavo National Park and possible factors influencing it. *J. Anim. Ecol.* **45**, 425–439.
Leuthold, W. (1977). "African Ungulates." Springer-Verlag, Berlin, Heidelberg, New York.
Leuthold, W. and Leuthold, B. M. (1975). Parturition and related behaviour in the African elephant. *Z. Tierpsychol.* **39**, 75–84.
Leuthold, W. and Sale, J. B. (1973). Movements and patterns of habitat utilization in elephants in Tsavo National Park Kenya. *E. Afr. Wildl. J.* **11**, 369–384.
Lewin, R. (1975). Poaching plague. *New Scientist* **65**, 938, 525–526.
Lippens, L. (1948). Congo four-tusker. *Field, London* **191**, 274.
Lull, R. S. (1908a). The evolution of the elephant. *Amer. J. Sci.* **4**, 25.
Lull, R. S. (1908b). The evolution of the elephant. Report. Smithsonian Institution, Washington.
Lydekker, R. (1907). The ears as a race character in the African elephant. *Proc. Zool. Soc. London* **1907**, 380–403.
Lydekker, R. (1926). "The Game Animals of Africa." Rowland Ward, London and Nairobi.
Lyell, D. D. (1924). "The African Elephant and its Hunters." London.
Maberry, M. B. (1963). Breeding Indian elephants *Elephas maximus* at Portland Zoo. *Int. Zoo Yearbook* **4**, 80–83.
Macinnes, D. G. (1942). Miocene and post-Pliocene Proboscidea from East Africa. *Trans. Zool. Soc. London* **25**, 33–106.
Macphail, J. G. S. (1930). The Bandala method of hunting elephant on foot. *Sudan Notes* **13**, 279–283.
Maglio, V. J. (1969). The status of the East African elephant *Archidiskodon exoptatus* Dietrich 1942. *Breviora Cambridge Mass.* **336**, 1–25.
Maglio, V. J. (1970a). Four new species of Elephantidae from the Plio-Pleistocene of Northwestern Kenya. *Breviora Cambridge Mass.* **15** 341, 1–43.
Maglio, V. J. (1970b). Early Elephantidae of Africa and a tentative correlation of African Plio-Pleistocene deposits. *Nature, London* **225** (5230), 328–332.

Maglio, V. J. (1971). The nomenclature of intermediate forms; an opinion. *Syst. Zool.* **20** (3), 370–373.
Maglio, V. J. (1972a). Vertebrate faunas and chronology of Hominid-bearing sediments East of Lake Rudolph Kenya. *Nature, London* **239** (5372), 379–385.
Maglio, V. J. (1972b). Evolution of mastication in the Elephantidae. Dept. Geol. Geophysic. Sci. Princeton University.
Maglio, V. J. (1973a). Origin and evolution of the Elephantidae. *Trans. Amer. Phil. Soc.* **63**, 3.
Maglio, V. J. (1973b). Evolution and mastication in Elephantidae. *Evolution* **26** (4), 638–658.
Maglio, V. J. (1974a). A new Proboscidean from the late Miocene of Kenya. *Palaeontology* **17** (3), 699–705.
Maglio, V. J. (1974b). Late tertiary fossil vertebrate successions in the Northern Gregory Rift East Africa. *Ann. Geol. Surv. Egypt* **4**, 269–286.
Maglio, V. J. (1976). Emergence of Pliocene epoch at Lothagam Hill East Africa. (Reprint Nat. Geogr. Soc. Res. Reports 1968.)
Maglio, J. V. and Hendey, Q. B. (1971). New evidence relating to the supposed Stegolophodont ancestory of the Elephantidae. *S. Afr. Archaeol. Bull.* **25**, 85–87.
Maloiy, G. M. O. (1965). African game animals as a source of protein. *Nut. Abstr. Rev.* **35**, 903–908.
Martin, A. (1963). Largest recorded elephant. *Afr. Wildlife* **17** (1), 80.
Maydon, H. C. (1951). "Big Game Shooting in Africa." London.
McCullagh, K. G. (1969a). The growth and nutrition of the African elephant I. Seasonal variations in the rate of growth and the urinary excretion of hydroxyproline. *E. Afr. Wildl. J.* **7**, 85–90.
McCullagh, K. G. (1969b). The growth and nutrition of the African elephant II. The chemical nature of the diet. *E. Afr. Wildl. J.* **7**, 91–97.
McCullagh, K. G. (1970). Arteriosclerosis in the African elephant. PhD. thesis Cambridge University.
McCullagh, K. G. (1973). Are African elephants deficient in essential fatty acids? *Nature, London* **242**, 267–268.
McGaughey, C. A. (1963). Musth. *Ceylon Vet. J.* **11**, 105.
McKay, G. M. (1971). The behaviour and ecology of elephants in Eastern Ceylon. PhD. thesis University of Maryland.
Melland, F. (1938). "Elephants in Africa." London.
Miall, L. C. and Greenwood, F. (1878). The anatomy of the Indian elephant. *J. Anat. Physiol. London* **12**, 385–400.
Milroy, A. J. W. (1949). A short treatise on the management of elephants and the management of elephant catching operations in Assam. Shillong.
Mitchell, B. L. (1963). A possible visual signal by the elephant. *Puku* **1**, 217.
Mitchell, P. C. (1905). On the intestinal tract of mammals. Order Proboscidea. *Trans. Zool. Soc. London*, 466–467.
Mohr, E. (1966). Pneumatisierung des Elefanten Schadels. *Sber. Ges. Naturf. Freunde Berlin (NF)* **6**, 77–82.
Moller, J. (1967). Catching elephants with a helicopter. *Animals* **9**, 692–694.
Morewood-Dowsett, J. (1939). Elephant past and present. *Suppl. J. R. Afr. Soc.* **38**, 152, 1–40. London.

Morrison-Scott, T. C. S. (1937). Naturally shed elephant molars. *Proc. Linn. Soc. London* **149**, 140–142.
Morrison-Scott, T. C. S. (1938). On the occurrence of a presumed first milk molar (MM 1) in African elephants. *Proc. Zool. Soc. London* **108**, 711–713.
Morrison-Scott, T. C. S. (1947). A revision of our knowledge of African elephant's teeth with notes on forest and "pigmy" elephants. *Proc. Zool. Soc. London* **117**, 505–527.
Mosby, H. S. (1963). Elephant management schemes: wildlife investigations techniques. *Publ. Wild Life Soc.* 220–222.
Moss, C. (1976). "Portraits in the Wild." Collins, London.
Myers, N. (1975). Tsavo National Park Kenya and its elephants. An interim appraisal. *Biol. Conserv.* **5**, 123–132.
Napier-Bax, P. and Sheldrick, D. L. W. (1963). Some preliminary observations on the food of elephants in the Tsavo National Park, Kenya. *E. Afr. Wildl. J.* **1**, 40–53.
Neumann, A. H. (1898). "Elephant Hunting in East Equatorial Africa." London.
Newton, R. F. (1958). Elephant census. *Uganda Wildlife and Sport* **1** (3), 28–30.
Nicholson, A. J. (1933). The balance of animal populations. *J. Anim. Ecol. Suppl.* **2** (1), 132.
Nicolson, B. D. (1952). Notes on the African elephant. *Afr. Wildlife* **6**, 361–365.
Nicolson, B. D. (1954). The African elephant. *Afr. Wildlife* **8**, 190–197.
Nicolson, B. D. (1955). The African elephant. The tuskless "Boody". *Afr. Wildlife* **9**, 31–40.
Nielsen, A. (1965). Die Muskulatur der Vorgleidmassen bei *Elephas Indicus. Anat. Anz.* **117**, 171–192.
Nilakanth of Rajamangalam (1931). The elephant lore of the Hindus. The Elephant sport (Matanga-lila of Nilakantha.) Trans. F. Edgerton Yale Univ. Press.
Noack, T. (1906). A dwarf form of the African elephant. *Ann. Mag. Nat. Hist.* **17**, 501–503.
Norton-Griffiths, M. (1975). The numbers and distribution of large mammals in Ruaha National Park Tanzania. *E. Afr. Wildl. J.* **13**.
Offermann, P. P. M. (1949). Les grand troupeaux d'éléphants de l'Uélé. *Bull. Cps. Lieut. Ch. Congo Belge* **2**, 11–17.
Offermann, P. P. M. (1953). The elephant in the Belgian Congo. *In* "The Elephant in East Central Africa." Rowland Ward. London and Nairobi.
Osborn, H. F. (1900). "The angulation of the limbs of Proboscidea Dinocerata and other quadrupeds in adaption to weight." Boston.
Osborn, H. F. (1934). Evolution and geographic distribution of the Proboscidea; moeritheres, dinotheres and mastodonts. *J. Mammal.* **15**, 177–184.
Osborn, H. F. (1936–42). Proboscidea: A monograph of the discovery, evolution, migration and extinction of the mastodonts and elephants of the world. *Ann. Mus. Nat. Hist. New York.*
Osborn, H. F. (1942). "Proboscidea Stegodontoidea, Elephantoidea" 1198. New York.

Owen, R. (1840–45) "Odontography, Treatise on the Comparative Anatomy of the Teeth." London.

Owen-Smith, N. (1966). The incidence of tuskless elephants in Mana Pools Game Reserve. *Afr. Wildlife* **20**, 69–73.

Parker, I. S. C. (1964). The Galana Game Management Scheme. *Bull. Epizoot. Dis. Afr.* **12**, 21–31.

Parker, I. C. S. and Archer, A. L. (1970). The status of elephant, other wildlife and cattle in Mkomazi Game Reserve. *Wildlife Services Ltd. Report to Tanzania Govt.*

Parker, I. C. S. and Graham, A. D. (1971). The ecological and economic basis for game ranching in Africa. *In* "The Scientific Management of Animal and Plant Communities for Conservation." (Duffey, E. and Watt, A. S. eds.) Blackwell, Oxford.

Perry, J. S. (1949). An investigation of East African elephants. *Proc. Zool. Soc. London* **119**, 606.

Perry, J. S. (1952). The growth and reproduction of elephants in Uganda. *Uganda J.* **16**, 51–66.

Perry, J. S. (1953). The reproduction of the African elephant *Loxodonta africana*. *Phil. Trans. Roy. Soc.* B **643**, 237.

Perry, J. S. (1954). Some observations on growth and tusk weight in male and female African elephants. *Proc. Zool. Soc. London* **124**, 97–104.

Perry, J. S. (1964). The structure and development of the reproductive organs of the female African elephant. *Phil. Trans. Roy. Soc.* B **248**, 35–51.

Perry, J. S. (1974). Implantation, foetal membranes and early placentation of the African elephant *Loxodonta africana*. *Phil. Trans. Roy. Soc.* **269**, 109–135.

Petrides, G. A. and Swank, W. G. (1965). Population densities and the range-carrying capacity for large mammals in Queen Elizabeth National Park, Uganda. *Zool. Africana* **1** (1), 209–225.

Petrides, G. A. and Swank, W. G. (1966). Estimating the productivity and energy relations of an African elephant population. *In* 9th Int. Conf. Grassland Prof. Alarico, San Paulo, Brazil.

Petrocchi, C. (1941). Il giacimento fossilifero di Sahabi. *Boll. Soc. Geol. Ital.* **60** (1), 107–114.

Pfaff, G. (1940). Reports on the investigation of diseases of elephants. Vet. Dept. Burma, Rangoon.

Pfeffer, P. (1960). Sur la validité des formes naines de l'éléphant d'Afrique. *Mammalia* **24** (4), 556–576.

Philippson, P. (1934). Domesticating the African elephant. Experiments in the Belgian Congo. *Field, London* **163**, 1527.

Phillips, J. F. V. (1925). The Knysna elephants, a brief note on their history and habits. *S. Afr. J. Sci.* **22**, 287–293.

Piana, G. P. and Stazzi, P. (1909) Trematodes parasites de l'éléphant d'Afrique. *C.R. Ass. fr. Avanc. Sci.* **37**, 580.

Pienaar, U de V. (1967). Operation "Komandhopfu." *Koedoe* **10**, 158–164.

Pienaar, U. de V., Wyk, P. van and Fairall, N. (1966). An aerial census of elephant and buffalo in the Kruger National Park and the implications thereof on intended management schemes. *Koedoe* **9**, 40–107.

Pitman, C. R. S. (1934). A report on a faunal survey of Northern Rhodesia with especial reference to game, elephant control and National Parks, Govt. Printer, Livingstone.

Pliny (1855). The natural history of Pliny. "The nature of terrestrial animals—Elephants." Translation J. Bostock and H. T. Riley.

Pohle, H. (1926). Notizien über Afrikanische Elefanten. *Z. Säugetierk.* **1**, 58–64.

Poles, W. E. (1955). Courtship of African elephants. *Oryx* 3, 71–74.

Poles, W. E. (1960). Courtship of African elephants. *Black Lechwe* **2** (4), 105–110

Poppleton, F. (1957). An elephant birth. *Afr. Wildlife* **2**, 106–108.

Priezac S. de (1650). L'Histoire des éléphants. Paris.

Quick, H. (1965). Ecology of the African elephant. BSCS Pamphlet 21. D. C. Heath, Boston.

Rees, A. F. (1963). Some notes on elephants and their feeding habits. *Tanganyika Notes and Records* **61**, 205–208.

Rice, D. W. (1964). Birds associating with elephants and hippopotamuses. *Auk* **80**, 196–197.

Robertson-Bullock, W. (1962). The weight of the African elephant *Loxodonta africana Proc. Zool. Soc. London* **138** (1), 133–135.

Rodhain, J. (1928). Les oestres de l'éléphant. *Bull. Cer. Zool. Congol.* **4**, 91–92.

Roosevelt, T. and Heller, E. (1915). "Life Histories of Game Animals." London.

Ross, I. C. (1969). Game distribution in the Kidepo Valley National Park. *E. Afr. Wildl. J.* **7**, 171–174.

Ross, I. C., Field, C. R. and Harrington, G. N. (1976). The savanna ecology of the Kidepo Valley National Park III. *E. Afr. Wildl. J.* **14**, 35–48.

Roth, H. H. (1964). Game utilization in Rhodesia in 1964. *Mammalia* **30**, 397–424.

Roth, H. H. and Austen, B. (1966). Twin calves in elephants. *Säugetierk Mitt.* **14**, 342–345.

Rushby, G. G. (1953). The elephant in Tanganyika. *In* "The elephant in East Central Africa." (Hill, W. C. O. *et al.*, eds), London.

Rushby, G. G. (1965). "No more the Tusker." London.

Sanderson, G. P. (1878). "Thirteen years among the wild beasts of India, their haunts and habits from personal observation with an account of the modes of capturing and taming elephants." London.

Savidge, J. M. (1964). "Elephant in the Kidepo Valley National Park." Mimeo Report to Uganda National Parks.

Savidge, J. M. (1965). In the footsteps of the elephants. *Oryx* **8**, 163.

Savidge, J. M. (1966). Change in population number and reproductive rate of elephants in Uganda. *J. Wildl. Mgmt* **30**, 791–809.

Savidge, J. M. (1968). Elephants in the Ruaha National Park Tanzania. Management problem. *E. Afr. Agric. For. J.* 33, 191–196.

Schaub, S. (1948). Das Gebiss der Elefanten. *Verh. naturf. Ges. Basel* **59**, 89–112.

Schneider, R. (1956). Untersuchungen über den Feinbau der Schlafendruse beim Afrikanischen and Indischen Elefanten. *Acta Anat.* **28**, 303–312.

Schouteden, H. (1947). "De Zoogdieren van Belgisch Congo en van Ruanda-Urundi." Tervuren, Belgium.

Schulte, T. L. (1937). The genito-urinary system of the *Elephas indicus* male. *Amer. J. Anat.* **61**, 131–157.

Seideman, R. M. and Wheeler, K. M. (1947). Elephant tusks. A source of human anthrax. *J. Amer. Med. Ass.* **135** (13), 837–838.

Seth-Smith, A. M. D. and Parker, I. S. C. (1967). A record of twin foetuses in the African elephant. *E. Afr. Wildl. J.* **5**, 167.

Sheldrick, D. (1966). "The Orphans of Tsavo." London.

Sheldrick, D. (1972). Death of the Tsavo elephants. *Sat. Rev. Sci. New York* **1**, 31.

Sheldrick, D. (1973). "The Tsavo Story." Collins and Harvill Press, London.

Sheldrick, D. (1975). *Africana* **5** (11).

Shelton, D. J. (1965). Some observations on elephants. *Afr. Wildlife* **19** (2).

Sherborn, C. D. (1935). The elephant before A.D. *Ann. Nat. Hist.* **15** (10), 492–495.

Shimizu, Y., Fujita, T. and Isokawa, S. (1960). Anatomy of a female Indian elephant with reference to its visceral organs. *Acta Anat. Nippon* **35**, 261.

Short, R. V. (1962). The peculiar lungs of the elephant. *New Scientist* **16**, 570–572.

Short, R. V. (1964). Anthrax in Chester Zoo. *Vet. Rec.* **76** (37), 1040.

Short, R. V. (1966). Oestrus behaviour, ovulation and formation of *corpus luteum* in the African elephant Loxodonta africana. *E. Afr. Wildl. J.* **4**, 56–68.

Short, R. V. (1969). Notes on the teeth and ovaries of an African elephant *Loxodonta africana* of known age. *J. Zool. London* **158**, 421–425.

Short, R. V. and Buss, I. O. (1965). Biochemical and histological observations on the *corpora lutea* of the African elephant *Loxodonta africana*. *J. Reprod. Fert.* **9**, 61.

Short, R. V., Mann, T. and Hay, M. F. (1967). Male reproductive organs of the African elephant *Loxodonta africana*. *J. Reprod. Fert.* **13**, 517–536.

Sikes, S. K. (1968). The African elephant *Loxodonta africana*: a field method for the estimation of age. *J. Zool. London* **154**, 235–248.

Sikes, S. K. (1969). Habitat and cardiovascular disease: Observations made in East Africa on free-living wild animals, with particular reference to the African elephant. *Trans. Zool. Soc. London* **32** (1), 1–104.

Sikes, S. K. (1971). "The Natural History of the African elephant." Weidenfeld and Nicolson, London.

Siller, F. C. and Meyler, R. M. (1968). "Elephants Ancient and Modern." Viking Press, New York.

Simon, N. (1962). "Between the Sunlight and the Thunder." London.

Smith, J. G., Hanks, J. and Short, R. V. (1969). Biochemical observations on the *corpora lutea* of the African elephant *Loxodonta africana*. *J. Reprod. Fert.* **20** (1), 111–120.

Somander, S. V. O. (1963). Wild elephants as water diviners. *Loris* **9**, 1962, 244–246.

Spinage, C. A. (1959). An apparent case of precocious tusk growth in a young African elephant. *Proc. Zool. Soc. London* **133**, 45.

Spinage, C. A. (1960). An unusual threat display of elephant. *J. E. Afr. Nat. Hist. Soc.* **23**, 243.

Spinage, C. A. (1972a). A review of ivory exploitation and elephant population trends in Africa. *E. Afr. Wildl. J.* **11**, 281–289.

Spinage, C. A. (1972b). Evolution of the Proboscidea. *Sonderdruck aus Säugetierk. Mitt.* **1972**.

Sprinz, R. (1952). The innervation of the trunk of an Indian elephant. *Proc. Zool. Soc. London* **122**, 621–623.

Steel, J. H. (1885). "A Manual of the Diseases of the elephant." Madras.

Stewart, D. R. M. and Stewart, J. (1963). The distribution of some large mammals in Kenya. *J. E. Afr. Nat. Hist. Soc.* **24**, 1–25.

Stigand, C. H. (1913). "Hunting the Elephant in Africa and other recollections of thirteen-years wanderings." New York.

Stuckeley, W. (1722). An essay towards the anatomy of the elephant from one dissected at Fort St. George, October 1715 and another at London October 1720. Appendix *In* "Of the Spleen its Description and History." London.

Sunamoto, E. (1931–32). "The Elephant." 2 vols, Osaka.

Sunderland, J. (1912). "Adventures of an Elephant Hunter." London.

Swart, E. R. (1963). Age of the baobab tree. *Nature, London* **198**, 708–709.

Swynnerton, C. F. M. (1924). "Report on the control of elephants in Uganda." Entebbe.

Temple-Perkins, E. A. (1955). "Kingdom of the Elephant." Andrew Melrose, London.

Thomas, A. S. (1940). Grasses as indicator plants in Uganda. *E. Afr. Agric. J.* **6**, 19–22; 77–80.

Thomas, A. S. (1942). Note on the distribution of *Chlorophora excelsa*. *Emp. For. J.* **21**, 42–43.

Toldt, K. (1913). Über die aussere Korpergestalt eines Foetus von *Elephas maximus*. *Anz. Akad. Wiss. Wien* **50**, 302–304.

Turner, M. I. and Watson, M. (1964). A census of game in Ngorongoro Crater. *E. Afr. Wildl. J.* **2**, 165.

Valen, van L. (1969). Evolution of communities and late Pleistocene extinctions. *Proc. N. Amer. Palaeont. Conv. Part E*, 469–485.

Verheyen, R. (1954). Elements pour une monographie éthologique de l'éléphant d'Afrique *Loxodonta africana* Blumenbach. *Bull. Inst. Roy. Congo Belge* **30**, 1–19.

Verheyen, R. (1960). Sur la morphologie et le remplacement des molaires chex l'éléphant d'Afrique *Loxodonta africana*. *Bull. Inst. Roy. Sci. Nat. Belg.* **36**, 1–18.

Vesey-Fitzgerald, D. F. (1965). The utilisation of natural pastures by wild animals in the Rukwa Valley Tanganyika. *E. Afr. Wildl. J.* **3**, 38–48.

Vesey-Fitzgerald, D. F. (1968). An experiment in adapting an electric fence to elephant behaviour. *E. Afr. Agr. For. J.* **1968**, 185–190.

Vesey-Fitzgerald, D. F. (1969). Utilization of the habitat by buffalo in Lake Manyara National Park. *E. Afr. Wildl. J.* **7**, 131–145.

Vesey-Fitzgerald, D. F. (1972). A survey of the animal impact on trees and shrubs and plant succession in the Lake Manyara National Park. Typescript on file S.R.I. Library.

Ward, R. (Ed.) (1953). "The Elephant in East Central Africa." A. Monograph. Rowland Ward, London and Nairobi.
Watson, D. M. S. (1946). The evolution of the Proboscidea. *Biol. Rev.* **21**, 15–29.
Watson, M. (1874). Use of the mouth and trunk in drinking. *In* Contributions to the anatomy of the Indian elephant. *J. Anat. Phys. London* **8**, 90.
Watson, R. M. and Bell, R. H. V. (1965). Elephant count in Tsavo National Park (East), Typescript 6 pp.
Watson, R. M. and Bell, R. H. V. (1969). The distribution, abundance and status of the elephant in the Serengeti region of Northern Tanzania. *J. Appl. Ecol.* **6** (2), 115–132.
Watson, R. M. and Turner, M. I. M. (1965). A count of the large mammals of the Manyara National Park. *E. Afr. Wildl. J.* **3**.
Watson, R. M., Graham, A. D. and Parker, I. C. S. (1969a). A census of the large mammals of Loliondo controlled area, Northern Tanzania. *E. Afr. Wildl. J.* **7**, 43–59.
Watson, R. M., Parker, I. S. C. and Allan, T. (1969b). A census of elephant and other large mammals in the Mkomazi region of Northern Tanzania. *E. Afr. Wildl. J.* **7**, 11–26.
Watson, R. M., Bell, R. H. V. and Parker, I. S. C. (1972). Men and Elephant. *Africana* **4** (11), 20–21.
Weir, J. S. (1972a). Exploitation of water-soluble sodium by elephants in Murchison Falls National Park Uganda. *E. Afr. Wildl. J.* **11**, 1–7.
Weir, J. S. (1972b). Mineral content of African elephant dung. *E. Afr. Wildl. J.* **10**, 229–230.
Weir, J. S. (1972c). Spatial distribution of elephants in an African National Park in relation to environmental sodium. *Oikos* **23**, 1.
Weir, J. S. and Davison, E. (1965). Daily occurrence of African game animals at waterholes during dry weather. *Zool. Africana* **1**, 353–368.
Wetzel, H. (1969). Myasis flies (*Dipetra*, *Calliphoridae*, *Oestridae*, *Gasterophilidae*) of the African and Indian elephant. *Z. Angew. Zool.* **56**, 489–502.
Whitaker, J. (1794). "The Course of Hannibal over the Alps Ascertained." London.
Williams, J. H. (1953). "Bandoola." Hart Davis, London.
Williams, J. H. (1956). "Elephant Bill." Hart Davis, London.
Wing, L. D. and Buss, I. O. (1970). "Elephants and Forests." Wildlife Monograph 19. Wildlife Soc. Washington.
Winter, W. H. (1964). Elephant behaviour. *E. Afr. Wildl. J.* **2**, 163–164.
Wislocki, G. B. (1939). Notes on the hypophysis of an adult Indian elephant. *Anat. Rec.* **74**, 321–328.
Wislocki, G. B. (1940). The topography of the hypophysis in the elephant, manatee and hyrax. *Anat. Rec.* **77**, 427–445.
Woodford, M. H. and Trevor, S. (1970). Fostering a baby elephant. *E. Afr. Wildl. J.* **8**, 204–205.
Wright, A. (1964). Mating habits of elephants. *Afr. Wildlife* **18** (4), 301–302.
Wyatt, J. R. and Eltringham, S. K. (1974). Daily activity of the elephant in the Ruwenzori National Park Uganda. *E. Afr. Wildl. J.* **12**.

Wynne-Edwards, V. C. (1962). "Animal dispersion in relation to social behaviour." Oliver and Boyd, Edinburgh.
Young, J. Z. (1950). "Life of the Vertebrates." Clarendon Press, Oxford.
Zvetaera, N. P. (1940). The pathology of the elephant. *Proc. Moscow Zool.* **1**.

Perissodactyls

Alexander, F. (1952). Some function of the large intestine of the horse. *Quart. J. Exp. Physiol.* **37**, 205–214.
Alexander, F. (1963). Digestion in the horse. *In* "Progress in Nutrition and Allied Sciences" (Cuthbertson, ed.) pp. 259–268. Oliver and Boyd, Edinburgh.
Alexander, A. and Player, I. C. (1965). A note on the nuchal hump of the square-lipped rhinoceros. *Lammergeyer* 3 (2), 5–9.
Allen, J. A. (1909). Mammals from British East Africa collected by the Tjader Expedition of 1906. *Bull. Amer. Mus. Nat. Hist.* **26**, 147.
Altmann, M. (1951). The study of behaviour in a horse and mule group. *Sociometry* **14**, 351–366.
Anderson, G. D. and Talbot, L. M. (1965). Soil factors affecting distribution of the grassland types and their utilization by wild animals on the Serengeti Plains Tanganyika. *J. Ecol.* **53**, 1.
Ansell, W. F. H. (1967). Perissodactyla. *In* "Preliminary Identification Manual for African Mammals." (Meester, J. ed.), Smithsonian Institution, Washington.
Antonius, O. (1937). Über Herdenbildung und Paarungseigentümlichkeiten der Einhufer. *Z. Tierpsychol.* **1**, 259–289.
Antonius, O. (1938). On the geographical distribution in former times and today of the recent Equidae. *Proc. Zool. Soc. London* **107** (4), 557–564.
Antonius, O. (1940). Beobachtungen an Einhufern in Schönbrunn XVI. Über das Damarazebra (*Equus quagga antiquorum*). *Zool. Gart.* (*NF*) *Leipzig* **12**, 247–257.
Antonius, O. (1951). Die Tigerpferde die Zebras. *Mongr. Wildsäugetiere* **11**, 1–148.
Antony, H. (1929). Horns and antlers; their occurrence, development and function in the Mammalia. *New York Zool. Soc. Bull.* **32**, 2–33.
Arambourg, C. (1956). Sur des restes *d'Hipparion sitifense* Pomel, des calcaires lacustres de Mascara. *Bull. Soc. Geol. Fr.* **6** (6), 817–827.
Arambourg, C. (1959). Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord. *Mém. Ser. Carte Géol. Algerie N.S. Paléont.* **4**, 161.
Arambourg, C. (1970). Les Vertébrès du Pléistocène de l'Afrique du Nord. Tome 1. Fasc. 1. Historique Stratography Paléontology (Proboscidiens et Perissodactyles). *Arch. Mus. Nat. Hist. Paris* **10** (7), 1–128.
Archer, M. (1971). Preliminary studies on the palatability of grasses, legumes and herbs to horses. *Vet. Rec.* **89**, 236–240.
Asdell, S. A. (1946). "Patterns of Mammalian Reproduction." Comstock, New York.
Azzaroli, A. (1965). The two Villafranchian horses of the Upper Valdarno. *Palaeontogr. Ital.* **59**, 29, 1–12.

Azzaroli, A. (1966). Pleistocene and living horses of the old world: an essay of a classification based on skull characters. *Paleontogr. Ital.* **61**, 1–15.

Azzaroli, A. (1970). Villafranchian correlations based on large mammals. *Giornale di geologia* (2), **35** (1), 1–21.

Babault, G. (1949). Notes éthologiques sur quelques mammifères africains. *Mammalia* **13**, (1 & 2).

Backhaus, D. (1960a). Wie Zebras kampfen. *Kosmos Stuttgard* **56**, 8–10.

Backhaus, D. (1960b). Über das Kampfverhalten beim Steppenzebra. *Tierpsychol.* **17**, 345–350.

Backhaus, D. (1964). Zum Verhalten des nördlichen Breitmaulnäshorns *Dicerossimum cottoni*, Lydekker 1908. *Zool. Gart.* (*NF*) *Leipzig*, **29**, 93–107.

Bakker, R. T. (1971). Dinosaur physiology and the origins of mammals. *Evolution* **25**, 636–658.

Balsom, E. (1963). The miracle of the Rukwa. *Africana* **1** (6), 12–13.

Balsom, E. (1967). Rukwa cropping scheme Tanzania Game Division Dar-es-Salaam. (Mimeographed Dar-es-Salaam.)

Balsom, E. (1971). Loliondo cropping project. Tanzania Game Division Mimeograph.

Bard, J. B. L. (1977). A unity underlying the different zebra striping patterns. *J. Zool. London* **183**, 527–539.

Barrow, sir J. (1801–4). Travels in the interior of Southern Africa in the years 1797–98.

Beddard, F. E. and Treves, F. (1889). On the anatomy of *Rhinoceros sumatrensis*. London.

Bell, R. H. V. (1969). The use of the herb layer by grazing ungulates in the Serengeti. PhD thesis, University of Manchester.

Bell, R. H. V. (1970). The use of the herbage by grazing ungulates in Serengeti *Br. Ecol. Soc. Symp.* **10**, 111–129.

Bell, R. H. V. (1971). A grazing ecosystem in the Serengeti. *Scient. Amer.* **225**, 86–93.

Benzon, B. (1948). Maneless Zebra. *Field London* **1948**.

Berlin, J. (1962). Significant spots. *Horse and Hound.* (Oct. 27).

Bigalke, R. C. (1968). The contemporary mammal fauna of Africa. *Quart. Rev. Biol.* **43**.

Bigalke, R. C., Steyn, T., De Vos, D. and Waard, K. (1950). Observations on a juvenile female white rhino *Ceratotherium simum* in the National Zoological Gardens of South Africa. *Proc. Zool. Soc. London* **12**, 519–528.

Bindernagel, J. A. (1975). Report on game management in the Loliondo, Rukwa and Yaida areas of the Republic of Tanzania. Mimeographed Report to Tanzania Game Department, Dar-es-Salaam.

Bishop, W. W., Chapman, G. R., Hill, A. and Miller, J. A. (1971). Succession of Cainozoic vertebrate assemblages from northern Kenya Rift Valley. *Nature, London* **233**.

Blaine, C. (1922). Notes on the zebras and some antelopes of Angola. *Proc. Zool. Soc. London* **1922**, 317.

Blakemore, C. (1971). Why we see what we see. *New Scientist* **51**, 614.

Blanchard, J. (1964). Informations recherchées d'après les Equidés européens figurés. Barcelone. Viking Fund Publications in Anthropology No. 39. New York.

Blancou, L. (1954). Notes sur les mammifères de l'Equateur français. Un Rhinoceros de forêt. *Mammalia* **18** (1), 358–363.

Boné, E. L. and Singer, R. (1965). Hipparion from Langebaanweg Cape Province and a revision of the genus in Africa. *Ann. S. Afr. Mus.* **48** (16), 273–397.

Bourdelle, M. E. (1940). La morphologie extérieure du pied chez les Equidés domestiques et sauvages. *Mammalia* **4**.

Bourdelle, M. E. (1940–41). Essai d'une étude morphologique des Equidés préhistoriques de France d'après les gravures rupestres. *Mammalia* **11** (1).

Bourdelle, M. E. (1941). Zèbres et Couaggas. *Bull. Soc. Nat. d'Acclimat.* **88**, 169–177.

Bourdelle, M. E. (1944). Chevaux, ânes et zèbres. *Bull. Conf. Soc. d'Acclimat. France* **91**, 49–71.

Bourdelle, M. E. (1949). La distribution géographique des Equidés actuels. *Int. Congr. Zool. Paris* **1948**, 383–387.

Bourdelle, M. E. (1956). Les parentés morphologiques des Equidés caballins d'après les gravures rupestres du Sud-ouest de la France. *Mammalia* **20**, 23–33.

Bourdelle, M. E. and Frechkop, S. (1950). La classification des Equidés actuels. *Mammalia* **14** (3), 126–137.

Brand, D. J. (1964). Distribution and numeral status of the status of the southern white rhinoceros *Ceratotherium simum* and the black rhinoceros *Diceros bicornis* in southern Africa. *Zoön.* **4**.

Breuil, H. and Lantier, R. (1951). "Les Hommes de la Pierre ancienne." Payot, Paris.

Brooks, A. C. (1959). The white rhinoceros in West Nile. Unpublished manuscript, Uganda Game Department.

Bruemmer, F. (1967). The wild horses of Sable Island. *Animals* **10**, 14–17.

Burtt, B. D. R. (1929). Fruit and seed dispersal by mammals in Singida. *J. Ecol.* **17** (2).

Cabrera, A. (1936). Subspecific and individual variation in the Burchell zebra *J. Mammal.* **17**, 89–112.

Camp, L. C. and Smith, N. (1942). Phylogeny and functions of digital ligaments of the horse. *Mem. Univ. California* **13**, 69.

Campbell, G. (1957). Rhino on two legs, (erect stance in browsing). *Field, London* **209**, 570.

Casebeer, R. L. and Koss, G. G. (1970). Food habits of wildebeest, zebra, hartebeest and cattle in Kenya Masailand. *E. Afr. Wildl. J.* **8**, 25.

Cave, A. J. E. (1962). The pedal scent gland in Rhinoceros. *Proc. Zool. Soc. London* **139**, 685–690.

Cave, A. J. E. (1964). The processus glandis in the Rhinocerotidae. *Proc. Zool. Soc. London* **143** (4), 569–586.

Cave, A. J. E. (1966). The preputial glands of *Ceratotherium*. *Mammalia* **30**, 153–159.

Cave, A. J. E. and Allbrook, D. B. (1959). The skin and nuchal eminence of the white rhinoceros. *Proc. Zool. Soc. London* **132**, 99–107.

Cave, A. J. E. and Aumonier, F. J. (1964). Lymph node structure in *Ceratotherium. J. Roy. Microsc. Soc.* **83**, 425–431.

Cleave, J. H. (1958). Maneless zebras. *Uganda Wildlife* **1** (3), 57–58.

Cobb, S. (1976). The distribution of the large herbivore community of Tsavo National Park Kenya. D.Phil. thesis, Oxford.

Cole, L. C. (1949). The measurement of interspecific association. *Ecology* **30** (4) 411–424.

Condy, P. (1973). The population, status, social behaviour and daily activity pattern of the white rhinoceros in the Kyle National Park Rhodesia. MSc. thesis, University Rhodesia.

Cooke, H. B. S. (1943). Cranial and dental characters of the recent South African Equidae. *S. Afr. J. Sci. Johannesburgh.* **40**, 254–257.

Cooke, H. B. S. (1950). A critical revision of the Quarternary Perissodactyla of Southern Africa. *Ann. S. Afr. Mus.* **31** (4), 34–479.

Cooke, H. B. S. and Coryndon, S. C. (1970). Pleistocene mammals from the Kaiso formation and other related deposits in Uganda. *In* "Fossil Vertebrates of Africa" Vol. 2 (Leakey, L. S. B. and Savage, R. J. G. eds.), pp. 107–224. Academic Press, London and New York.

Cullen, A. (ed.) (1969). African adventure. *In* "Window on to Wilderness." East Africa Publishing House, Nairobi.

Cushing, D. H. and Harden-Jones, P. R. (1968). Why do fish school? *Nature, London* **218**,

D'Arcy W. Thompson (1917). "On Growth and Form." Cambridge University Press. 918–920.

Darling, F. F. (1960a). "Wildlife in an African Territory." Oxford University Press.

Darling, F. F. (1960b). An ecological reconnaissance of the Mara Plains in Kenya Colony. *Wildlife Monogr.* **5**, 5–41.

Darwin, C. (1868). "The Variation of Animals and Plants under Domestication." John Murray, London.

Dasmann, R. F. and Mossman, A. S. (1962a). Abundance and population structure of wild ungulates in some areas of Southern Rhodesia, *J. Wildl. Mgmt.* 3.

Dasmann, R. F. and Mossman, A. S. (1962b). Population studies of impala in Southern Rhodesia. *J. Mammal.* **43**, 375–395.

Davies, J. (1952). The anatomy of a twenty-two millimetre embryo of the African rhino *Rhinoceros bicornis. Proc. Zool. Soc. London* **122**, 593–611.

De la Fuente, F. R. World of Wildlife I. "Hunters and Hunted of the Savannah." Orbis, London.

Deraniyagala, P. E. P. (1953). The extinct and living subfamilies of African Rhinocerotidae. *Spolia Zeylan* **27**, 13–14.

Dirschl and Wetmore (1978). "Grevy's Zebra Abundance and Distribution in Kenya, 1977." Ministry of Tourism and Wildlife. Aerial survey report series No. 4.

Dittrich, L. (1966). Männelose Zebras in Zoo Hanover. *Säug. Mitt.* **14** (2), 100–104.

Dittrich, L. (1967). Breeding the black rhinoceros *Diceros bicornis* at Hanover Zoo. *Int. Zoo Yearbook* **1**, 161–162.

Dobroruka, L. J. (1961). Ein Verhaltenstudie des Przewalski Urwildpferdes in dem Zoologischen Garten Prag. *Equus* **1**, 89–104.

Drummond, W. H. (1867). On the African Rhinoceroses. *Proc. Zool. Soc. London* **109**, 14.

Drummond, W. H. (1875). "The Large Game and Natural History of South and South-East Africa." Edmosten Douglas Edinburgh.

Edinger, T. (1948). Evolution of the horse brain. *Geol. Soc. America Mem.* **25**, Baltimore.

Eisemann, V. (1975). Nouvelles interprétations des restes d'Equidés (Mammalia, Perissodactyla) de Nihowan (Pléistocène inférieur de la Chine du Nord), *Equus teilhardi* nov. sp. *Geobios.* **8**, 125–134.

Eisemann, V. (1976). Le protostylide: valeur systématique et signification phylétique chez les espèces actuellès et fossiles du genre *Equus. Sonderdruck Säugetierk.* **41** (6), 349–365.

Eisemann, V. (in press). Preliminary note on the Equidae from the Koobi Fora formation Kenya. *In* "Earliest Man and Environments in the Lake Rudolph Basin." (Coppens, Y., Howell, C., Isaac, G., Leakey, R. eds.) University of Chicago Press, U.S.A.

Eisemann, V. (in press) "Equidae from Omo", *Ibidem.*

Eisemann, V. and Giuli, C. de (1974). Caractères distinctifs entre vrais Zèbres *Equus zebra* et Zèbres de Chapman *Equus burchelli antiquorum* d'après l'étude de 60 têtes osseuses. *Mammalia* 3, 509–543.

Ellis, R. (1958). In Cullen 1969.

Estes, R. D. (1967). Trials of a zebra herd stallion. *Natural History* **76**, 58–65.

Estes, R. D. (1974). Zebra offer clues to the way wild horses once lived. *Smithsonian* **5**, 100–107.

Ewart, J. C. (1899). The penycuick Experiments. Telegony and Reversion, London.

Ewart, J. C. (1904). On East-African zebras. *Proc. Zool. Soc. London* **1904**, 181–183.

Falconer, H. and Cautley, P. T. (1849) "Fauna antiqua Sivalensis." part 9 "Equidae, Ruminantia, Camelidae, Sivatherium," Smith Elder and Co., London.

Faust, R. (1958). Die Geburt eines Spitzmaulnäshornes *Diceros bicornis* in Frankfurt. *Zool. Gart.* (*NF*) **22**, 208–214.

Feist, J. D. (1971). Behaviour of feral horses in Pryor Mountains Wild Horse Range. Thesis Univ. Michigan, U.S.A.

Ferreira, G. B. (1942). Las Zebras. *Bull. Soc. Port. Cienc. Nat.* **13**. Suppl. 3, 600–602.

Fisher, J., Simon, N. and Vincent, J. (1969) "The Red Book, Wildlife in Danger." Collins, London.

Forstèn, A. M. (1968). Revision of the Palaearctic Hipparion. *Acta Zool. Fenn.* **119**, 1–134.

Forstèn, A. M. (1972). Hipparion primigenium from Southern Tunisia. *Notes Serv. Geol.* **35**; *Trav. Geol. Tunisienne* **51**, 7–28.

Forsyth Major, C. J. (1877–1880). Beiträge zur Geschichte der fossilen Pferde insbesondere Italiens. *Abh. Schwez. Paläont.* **4**.

Fosbrooke, H. (1975). "The White Rhino in Tanzania." UNEP, Dodoma, Tanzania.

Foster, G. B. (1961). The square-lipped rhinoceros. *Lammergeyer* **1** (1), 25–35.

Foster, G. B. (1965). Mortality and ageing of black rhinoceros in East Tsavo National Park Kenya. *E. Afr. Wildl. J.* 3, 118–119.

Foster, G. B. (1967). The square-lipped rhino, *Ceratotherium simum cottoni* L. *E. Afr. Wildl. J.* **5**.

Frame, G. W. (1971). The black rhinoceros. *Animals* (July 1971), 693–699.

Frame, G. W. and Goddard, J. (1970). Black rhinoceros vocalizations. *E. Afr. Wildl. J.* **8**, 207.

Friant, M. (1950). Recherches sur le télencéphale des Rhinoceridae. *Proc. Zool. Soc. London* **120**, 337–347.

Friant, M. (1955). A propos des mammifères d'Europe à l'époque secondaire. *Cahiers géologiques* **31**.

Gee, E. P. (1950–52). The great Indian one-horned rhinoceros. *Oryx* **1** (5), 224–227.

Gee, E. P. (1953). The life history of the great Indian one-horned rhinoceros, *Rhinoceros unicornis* Linn. *J. Bombay Nat. Hist. Soc.* **51**, 341–348.

Gee, E. P. (1959). The great Indian rhinoceros, *R. unicornis* in Nepal. *J. Bombay Nat. Hist. Soc.* **56**, 484–510.

Geist, V. (1966). The evolution of horn-like organs. *Behaviour* **27** (3–4), 175–214.

Geist, V. (1974). On the relationship of ecology and behaviour in the evolution of ungulates: theoretical considerations. *In* "The Behaviour of Ungulates and its Relation to Management." (Geist, V. and Walther, F. eds.), IUCN Publications No. 24.

Gibson J. J. (1966). "The Senses Considered as Perceptual Systems." New York.

Giuli, de C. (1972). On the type form of *Equus stenonis* Cocchi. *Paleont. Ital.* **68** (38), 35–39.

Glover, J. and Duthie, D. W. (1958). The apparent digestibility of crude protein by non ruminants and ruminants. *J. Agric. Sci.* **51**, 290–293.

Glover, P. E. and Sheldrick, D. L. W. (1964). An urgent research problem on the elephant and rhino populations of the Tsavo National Park Kenya. *Bull. Epiz. Dis. Afr.* **12**, 33–38.

Goddard, J. (1966). Mating and courtship of the black rhinoceros *Diceros bicornis* L. *E. Afr. Wildl. J.* **4**, 69–75.

Goddard, J. (1967a). Home range, behaviour and recruitment rates of two black rhinoceros populations. *E. Afr. Wildl. J.* **5**, 133–150.

Goddard, J. (1967b). The validity of censusing black rhinoceros populations from the air. *E. Afr. Wildl. J.* **5**, 18–23.

Goddard, J. (1968). Food preferences of two black rhinoceros populations. *E. Afr. Wildl. J.* **6**, 1–18.

Goddard, J. (1969a). Aerial census of black rhinoceros using stratified random sampling. *E. Afr. Wildl. J.* **7**, 104–114.

Goddard, J. (1969b). A note on the absence of pinnae in the black rhinoceros. *E. Afr. Wildl. J.* **7**, 178–180.

Goddard, J. (1970a). Age criteria and vital statistics of a black rhinoceros population. *E. Afr. Wildl. J.* **8**, 105–121.

Goddard, J. (1970b). Food preferences of black rhinoceros in the Tsavo National Park. *E. Afr. Wildl. J.* **8**, 141–161.

Goddard, J. (1970c). A note on age at sexual maturity in the wild black rhinoceros. *E. Afr. Wildl. J.* **8**, 205.

Gogan, P. J. P. (1973). Some aspects of nutrient utilization by Burchell's zebra *Equus burchelli boehmi* Matschie in the Serengeti-Mara region East Africa. M.Sc. Thesis, Texas A and M University.

Gowers, sir W. (1950). The classical rhinoceros. *Antiquity Glos.* **24**, 61–71.

Gray, J. E. (1873). On the dentition of Rhinoceroses and on the characters offered by their skulls. *Ann. Mag. Nat. Hist. London* **4**, 11 (65), 336–361.

Graziosi, P. (1956). "L'arte dell'antica eta' della pietra." Firenze.

Greed, R. E. (1960). The composition of the milk of the black rhinoceros. *Int. Zoo Yearbook* **2**, 106.

Gregory, W. K. (1926). The horse in the tiger skin. *Zool. Soc. Bull. New York* **29**, 111–133.

Gromova, V. (1949a). Histoire des chevaux (genre *Equus*) dans l'ancien monde, II Evolution et classification du genre. *Trudy Paléont. Inst. Akad. Nauk SSSR* **17** (2), 162.

Gromova, V. (1949b). Histoire des chevaux (genre *Equus*) de l'ancien monde. *Trans. 1955 Inst. Paléont. Acad. Sci. URSS* **7** (1), 373. (*French transl. Ann. Centre d'Etudes et de Doc. Paléont.* **13**.)

Gromova, V. (1952). The Hipparions genus *Hipparion* from materials of Tarakliya Pavlodar and elsewhere. *Trudy Pal. Inst. Moskva Etud. Doc. Pal.* **12**, 1–290.

Groves, C. P. (1974). "Horses, Asses and Zebras in the Wild." Ralph Curtis Books, Hollywood.

Groves, C. and Mazak, V. (1967). On some taxonomic problems of Asiatic wild asses; with the description of a new subspecies (Perissodactyla Equidae.) *Z. f. Säugetierk.* **32**, 321–355.

Grunberg, W. and Burtscher, H. (1968). Uber einepockenartige Krankheit beim Rhinoceros *Diceros bicornis*. *Zentbl. Vet. Med.* B **15**, 649–657.

Grzimek, B. (1944). Rangordnungversuche mit Pferden. *Z. Tierpsychol.* **5**, 481–497.

Grzimek, B. (1960a). Die gegenwartige Zahl der Nashörner auf der Erde. *Säugetierk. Mitt.* **8** (2), 21–25.

Grzimek, B. (1960b). Die Zuzammensetzung der Nashörnmilch. *Zool. Gart. Leipzig* **25**, 202–204.

Grzimek, B. (1960c). Attrappenversuche mit Zebras und Löwen in der Serengeti. *Z. Tierpsychol.* **17**, 351–357.

Grzimek, B. (1964). "Rhinos Belong to Everybody." Collins, London.

Guggisberg, C. A. W. (1966). "S.O.S. Rhino." André Deutsch, London.

Gwynne, M. D. and Bell, R. H. V. (1968). Selection of vegetation components by grazing ungulates in the Serengeti National Park. *Nature* **220**, 390–393.

Hafez, E. S. E. (1962). The behaviour of horses. *In* "The Behaviour of Domestic Animals." Ballière Tindall & Cox, London.

Hagenbeck, D. (1966). Report on the hand-rearing of an Indian rhinoceros at Hamburg Zoo. *Int. Zoo Yearbook* **6**, 82–87.

Haines, F. (1963). "Appaloosa, the Spotted Horse in Art and History." University of Texas Press.

Hamilton, P. H. and King, J. M. (1969). The fate of black rhinoceroses released in Nairobi National Park. *E. Afr. Wildl. J.* **7**, 73–84.

Harper, F. (1945). Extinct and vanishing mammals of the Old World. *Amer. Comm. for Int. Wildlife Protec.* **123** (I–XV), 1–850.

Harthoorn, A. L. (1967). Adaption to solar radiation by African large herbivores.

Harthoorn, A. M. and Lock, J. A. (1960). (Roneo) The rescue of Rhinoceroses at Kariba Dam. *Oryx* **5**, 352.

Hartmann, F. (1970). *Africana*, **4** (4).

Haughton, S. H. (1931). The fossil Equidae of South Africa. *Ann. S. Afr. Mus.* **28**, 407.

Hayes, C. (1964). The fight to save Uganda's white rhino. *Africana* **2** (1).

Haymann, R. W. (1956). The Rhinoceros. *Zoo Life* **11**, 2–6.

Heckler, B. (1971). Beitrag zur Ethologie des Islandpferdes. (Dissertation Giessen.)

Hediger, H. (1949). Saugetiere Territorien und ihre Markierung. *Bijdr. t.d. Dierkunde* **28**, 172–184.

Hediger, H. (1955). Geburt und Aufzucht eines Nashörns. *Umschau* **55**, 307–308.

Heller, E. (1913). "The White Rhinoceros." Smithsonian Institution, Washington.

Hendey, O. B. (1970a). A review of the geology and palaeontology of the Plio-Pleistocene deposits at Langebaanweg Cape Province. *Ann. S. Afr. Mus.* **56** (2), 75–117.

Hendey, O. B. (1970b). The age of the fossiliferous deposits at Langebaanweg Cape Province. *Ann. S. Afr. Mus.* **56** (3), 119–131.

Heppes, J. B. (1958). The white rhinoceros in Uganda. *Afr. Wildlife* **12**, 273–280.

Hiley, P. G. (1977). The thermoregulatory response of the rhinoceros (*Diceros bicornis* and *Ceratotherium simum*) and the zebra (*Equus burchelli*) to diurnal temperature change. *E. Afr. Wildl. J.* **15** (4), 337.

Hitchins, P. M. (1968). Some preliminary findings on the population structure and status of black rhinoceros (*Diceros bicornis* Linn.) in Hluhluwe Game Reserve Zululand. *Lammergeyer* **3** (9), 26–28.

Hitchins, P. M. (1969). Influence of vegetation types on sizes of home ranges of black rhino in Hluhluwe Game Reserve. *Lammergeyer* **3** (10) 81–85.

Hitchins, P. M. (1970). Field criteria for ageing immature black rhinoceros. *Lammergeyer* **3** (12), 48–55.

Hitchins, P. M. and Keep, M. E. (1970). Observations on skin lesions of the black rhinoceros (*Diceros bicornis* Linn.) in Hluhluwe Game Reserve Zululand. *Lammergeyer* **3** (12), 56–65.

Hitchins, P. M., Keep, M. E. and Rochat, K. (1972). The capture of black

rhinoceros in Hluhluwe Game Reserve and their translocation to the Kruger National Park. *Lammergeyer* **17**, 18–28.

Hoepen, E. C. N. van (1952). Die Stamlyn van die Zebras. *Paleont. Navors. Nas. Mus.* **2**, 25–37.

Hoffstetter, R. (1950). La structure des incisives inférieures chez les Equidés modernes. Importance dans la classification des Zèbres-Couaggas. *Bull. Mus. Hist. Nat.* **22**, 684–692.

Hoffstetter, R. (1952). Les mammifères Pléistocènes de la République de l'Equateur. *Mém. 66 Soc. Géol. Fr. NS* **31**, 1–391.

Holman, D. (1969). "Inside Safari Hunting." W. H. Allen, London.

Hooijer, D. A. (1946). Prehistoric and fossil rhinoceroses from the Malay archipelago and India. *Proefschrift, Leiden.*

Hooijer, D. A. (1949). Observations on a calvarium of *Equus sivalensis* Falconer et Cautley from the Siwaliks of the Punjab with craniometrical notes on recent Equidae. *Arch. Néer. de Zool.* **8** (3), 243–266.

Hooijer, D. A. (1966). Miocene rhinoceroses of East Africa. *In* "Fossil Mammals of Africa" 21; *Bull. Brit. Mus. Nat. Hist. Geol.* **13** (2), 117–190.

Hooijer, D. A. (1969). Pleistocene East Africa rhinoceroses. *In* "Fossil Vertebrates of Africa" Vol. 1. (Leakey, L. S. B. ed.) pp. 71–98. Academic Press, London and New York.

Hooijer, D. A. (1971). A new rhinoceros from the late Miocene of Loperot Turkana district Kenya. *Bull. Mus. Comp. Zool.* **142** (3), 339–392.

Hooijer, D. A. (1973). Additional Miocene to Pleistocene rhinoceroses of Africa. *Zool. Med. Mus. Leiden* **46**, 149–178.

Hooijer, D. A. (in press). Phylogeny of the rhinoceroses in Africa. *In* (Maglio, V. J. ed.).

Hooijer, D. A. (in press). "Mammalian Evolution in Africa." Princeton University Press.

Hooijer, D. A. and Maglio, V. J. (1973). The earliest Hipparion south of the Sahara in the late Miocene of Kenya. *Proc. Ken. Ned. Akad. v. Wet. Amsterdam* B **76**, 311–315.

Hooijer, D. A. and Maglio, V. J. (1974). Hipparions from the late Miocene and Pliocene of Northwestern Kenya. *Zool. Verhandl.* **134**, 1–32.

Hooijer, D. A. and Patterson, B. (1972). Rhinoceroses from the Pliocene of Northwestern Kenya. *Bull. Mus. Comp. Zool.* **144**, 1–26.

Hopkins, B. (1966). "Forest and Savanna." Heinemann, London.

Hopwood, A. T. (1937a). The former distribution of Caballine and Zebrine horses in Europe and Asia. *Proc. Zool. Soc. London* **106**, 897–912.

Hopwood, A. T. (1937b). Die fossilen Pferde von Oldoway. *Wiss. Ergebn. Oldoway Exped. 1913. (NF)* **4**, 111–136.

Hopwood, A. T. (1947). Contributions to the study of some African mammals. *J. Linn. Soc. Zool.* **41**.

Huntley, B. J. (1967). Wildlife in South Africa Series, *Ceratotherium simum* Burchell. Sem. BSC Wildl. Mgmt. Course, Pretoria University.

Hutchinson, G. E. and Ripley, S. D. (1954). Gene dispersal and the ethology of the Rhinocerotidae. *Evolution* **8**, 178–179.

Huxley, J. (1960). The conservation of wildlife and natural habitats in Central and Eastern Africa. UNESCO Publication.

Huxley, J. (1965). Serengeti: a living laboratory. *New Scientist* (Aug. 26).

Imanishi, K. (1950). Social life of semi-wild horses in Toimisaki. Summary for the three surveys undertaken in 1948–49. *Physiol. Ecol. Japan* **4**, 29–42.

Imanishi, K. (1953). Social life of semi-wild horses in Toimisaki. Horses in their winter quarters. *Ann. Anim. Psychol. Japan* 3, 1132.

Ionides, C. J. P. (1953). Nature notes (1). *Afr. Wildlife* **7**, 127–135.

Jackson, F. J. (1894). The rhinoceros. *In* "Big Game Shooting", Badminton Library of Sports and Pastimes, London.

Jacobi, E. F. (1957). Recuperative power of the horn of the black rhinoceros. *Zool. Gart. Leipzig* **23**, 225–227.

Janis, C. (1976). The evolutionary strategy of the equidae and the origins of rumen and caecal digestion. *Evolution* **30**, 757–774.

Joleaud, L. (1933). Un nouveau genre d'Equidé quaternaire de l'Omo: *Libyhipparion aethiopicus*. *C. R. Somm. Seanc. Soc. Géol. Fr.* **53**, 7–28.

Joubert, E. (1970). The taxonomic status of the black rhinoceros in South-West Africa. *Madoqua* **2**.

Joubert, E. (1972a). The social organisation and associated behaviour in Hartmann's zebra. *Madoqua* **1** (6), 17–56.

Joubert, E. (1972b). Mountain zebra behaviour. *Zool. Africana* **7**.

Joubert, E. (1972c). Activity patterns shown by Hartmann zebra *Equus zebra hartmannae* in South-West Africa with reference to climatic factors. *Madoqua* **1** (5).

Joubert, E. (1972d). Tooth development and age determination in the Hartmann zebra *Equus hartmannae*. *Madoqua* **1** (6).

Joubert, E. (1973). Habitat preference, distribution and status of the Hartmann zebra *Equus zebra hartmannae* in South-West Africa. *Madoqua* **1** (7).

Joubert, E. (1974). Notes on the reproduction in Hartmann zebra *Equus zebra hartmannae* in South-West Africa. *Madoqua* **1** (8).

Joubert, E. (1974a). Composition and limiting factors of a Khomas Hochland population of Hartmann zebra *Equus zebra hartmannae*. *Madoqua* **1** (8).

Joubert, E. (1974b). Size and growth as shown by pre- and post-natal development of the Hartmann zebra *Equus zebra hartmannae*. *Madoqua* **1** (8).

Joubert, E. and Eloff, F. C. (1971). Note on the ecology and behaviour of the black rhinoceros *Diceros bicornis* Linn. in South-West Africa. *Madoqua* **1** (3), 5–53.

Kapitzke, G. (1973). "Wildlebende Pferde. "Verlag Paul Parey, Berlin.

Kattinger, E. (1952). Bemerkungen über Tigerpferde. *Z. f. Säugetierk.* **17**, 115–122.

Keast, A. (1965). Interrelationships of two zebra species in an overlap zone. *J. Mammal.* **46** (1), 53–66.

King, J. M. (1965). A field guide to the reproduction of the Grant's zebra and Grevy's zebra. *E. Afr. Wildl. J.* 3, 99–117.

King, J. M. (1969). The capture and translocation of the black rhinoceros. *E. Afr. Wildl. J.* **7**, 115–130.

Klaits, B. G. (1972). The moving mesaxonic manus: A comparison of tapirs and rhinoceroses. *Mammalia* **36** (1), 126–145.

Klingel, H. (1964a). Beobachtungen am Steppenzebra *Equus quagga boehmi* Matschie. *Sonderdruck Verhandl. Zool. Gesell, Kiel* **1964**.

Klingel, H. (1964b). Zur Sozialstructur des Steppenzebras *Equus quagga*. *Naturwiss.* **51**, 347.

Klingel, H. (1965a). Notes on the biology of the plains zebra *Equus quagga boehmi* Matschie. *E. Afr. Wildl. J.* **3**, 86–88.

Klingel, H. (1965b). Notes on tooth development and ageing criteria in the plains zebra *Equus quagga boehmi* Matschie. *E. Afr. Wildl. J.* **3**, 27–29.

Klingel, H. (1967). Soziale Organisation und Verhalten freilebender Steppenzebras. *Z. Tierpsychol.* **24**, 580–624.

Klingel, H. (1968a). Investigations on the social organisation and population ecology of the plains zebra *Equus quagga*. *Zool. Afr.* **4**, 240–263.

Klingel, H. (1968b). Soziale Organisation und Verhaltenweisen von Hartmann und Bergzebras *Equus zebra hartmannae* and *Equus zebra zebra*. *Z. Tierpsychol.* **25**, 76–88.

Klingel, H. (1968c). Das Sozialleben der Steppenzebras. *Naturwiss. u. Med.* **24**, 10–21.

Klingel, H. (1969a). Dauerhafte Sozialverbande beim Bergzebra. *Z. Tierpsychol.* **26**, 965–966.

Klingel, H. (1969b). Grevy's zebra project. *Africana* **3** (12), 35–36.

Klingel, H. (1969c). Reproduction in the plains zebra *Equus burchelli boehmi*: Behaviour and ecological factors. *J. Reprod. Fert. Suppl.* **6**, 339–345.

Klingel, H. (1969d). Zur Soziologie des Grevy-Zebras. *Zool. Anz. Suppl.* **33**, 311–316.

Klingel, H. (1972). Social behaviour of African Equidae. *Zool. Afr.* **7** (1), 175–185.

Klingel, H. (1974a). Zebras. *Newsletter Wildlife Clubs Kenya.*

Klingel, H. (1974b). A comparison of the social behaviour of the Equidae. *In* "The Behaviour of Ungulates and its Relation to Management." (Geist, V. and Walther, F. eds.) IUCN Publications No. 24.

Klingel, H. and Klingel, U. (1966a). Die Geburt eines Zebras. *Z. Tierpsychol.* **23**, 72–76.

Klingel, H. and Klingel, U. (1966b). Tooth development and age determination in *Equus quagga boehmi*. *Zool. Gart. Leipzig* **33**, 34–54.

Klingel, H. and Klingel, U. (1966c). The rhinoceroses of Ngorongoro Crater. *Oryx* **8** (5), 302–306.

Kreag, K. K. (1966). Hand-rearing of black rhinoceros. *Int. Zoo. Yearbook* **6**, 87–88.

Krumbiegel, I. (1961). Einfarbigkeit als ruckbildungvorgang, nach einer Beobachtung an Grantzebra. *Säugetierk. Mitt.* **9**, 1–4.

Krumbiegel, I. (1962). Quelienstudien über Asiatische Nashörne. *Säugetierk. Mitt.* **10**, 1–2.

Kruuk, H. (1972). "The Spotted Hyaena." University of Chicago Press, U.S.A.

Kuiper, K. and Schneider, K. M. (1940). Zur Gestalt des Nashörn-Penis. *Zool. Gart. Leipzig* **17**, 288–291.

Kurten, B. (1968). "Pleistocene Mammals of Europe." Aldine, Chicago.

Lamprey, H. F. (1963). Ecological separation of the large mammal species in the Tarangire Game Reserve Tanganyika. *E. Afr. Wildl. J.* **1**, 63–92.

Lamprey, H. F. (1964). Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai steppe in Tanganyika. *E. Afr. Wildl. J.* **2**.

Lamprey, H. F. (1974). Management of flora and fauna in national parks. *In* "II World Conference on National Parks" (Elliott, sir H. ed.), pp. 237–257, IUCN Switzerland.

Lang, E. M. (1961). Beobachtungen am Indischen Panzernashörn (*Rhinoceros unicornis*). *Zool. Gart.* (*NF*) **25**, 369–409.

Lang, H. (1923). Recent and historical notes on the square-lipped rhinoceros. *J. Mammal.* **4** (3), 155–163.

Lang, H. (1924). Threatened extinction of the white rhinoceros. *J. Mammal.* **5** (3), 173–180.

Laurie, A. and Olivier, R. (1977). Pachyderms in peril. *New Scientist* (15 Sept.).

Lawick, van H. (1970). "Innocent Killers." Collins, London.

Lewin, R. (1975). Poaching plague. *New Scientist* (Feb. 27).

Lithgon, T. (1961). The possible extinction of rhino at the Ngorongoro Crater. *Afr. Wildlife* **15**, 162–165.

Lorenz, L. (1902). On the specimen of the Quagga in the Imperial Museum Natural History in Vienna. *Proc. Zool. Soc. London* **1902**.

Lydekker, R. (1904). Note on the skull and Markings of the quagga. *Proc. Zool. Soc. London* **1904**.

Lydekker, R. (1912). "The Horse and its Relatives." London.

Lydekker, R. (1922). A guide to the specimens of the horse family exhibited in the British Museum. Brit. Mus. (Nat. Hist.) London.

Lydekker, R. (1926). "The Game Animals of Africa." London.

Maccullagh, B. and Achard, P. L. (1969). Mortalities of black rhino. *Int. Zoo Yearbook* **9**, 139–142.

Macfadden, B. J. (1976). Cladistic analysis of primitive equids. *Systemat. Zool.* **25** (1), 1–14.

Macfarlane, W. V., Howard, B., Maloiy, G. M. O. and Hopcraft, D. (1972). Tritiated water in field studies of ruminant metabolism in Africa. Repr. Isotope studies on the physiology of domestic animals. I.A.E.A. Vienna.

Macgrew, P. O. (1944). An early Pleistocene (Blancan) fauna from Nebraska. *Field. Mus. Nat. Hist. Geol. Ser.* **9** (2), 33–66.

Mackenzie, P. Z. (1950). Black rhino on the Twij. *Field, London.*

Maglio, V. J. (1972). Vertebrate faunas and chronology of hominidal bearing sediments East of Lake Rudolph Kenya. *Nature, London* **239**, 379–385.

Maloiy, G. M. O. (1970). Water economy of the Somali donkey. *Amer. J. Phys.* **219** (5), 1522–1527.

Matthew, W. D. (1926). The evolution of the horse. *Quart. Rev. Biol.* **1**, 130–185.

Matthew, W. D. (1931). Critical observations on the phylogeny of the Rhinoceros. *Univ. Calif. Publ. Geol.* **20**, 1–9.

Mauny, R. (1957). Prehistoric distribution of some large mammals in the Sahara. Proceedings third Pan-African Congress on Prehistory. London.

Meinertz, T. (1972). Eine topographische Untersuchung uber die Facialismuskeln beim Nashorn, *Diceros bicornis*. *Gegenb. Morphol. Jhb.* **118** (2), 206–227.

Mentis, M. T. (1972). A review of some life history features of the large herbivores of Africa. *Lammergeyer* **16**, 1–78.
Menzies, J. I. (1951). Man and the zebra. *Oryx* **1**, 127–133.
Mitchell, B. L. (1966). The survival of an archaic vertebrate (*Diceros bicornis*) in central Africa. *The Pulm* **4**, 190–192.
Modell, W. (1969). Horns and antlers. *Scient. Amer.* **220**, 114.
Mohr, E. (1951). Ungewöhnliche Streifung bei Pferden.
Moir, R. J. (1965). The comparative physiology of ruminant-like animals. *In* "Physiology of Digestion in Ruminants." (Dougherty, R. W. ed.), Butterworths, London.
Mollon, J. (1974). After effects and the brain. *New Scientist*, **61**, 886.
Monod, T. (1933). Anes sauvages. *Terre et Vie Paris* 3, 451–454.
Montgomery, G. G. (1957). Some aspects of the sociability of the domestic horse. *Trans. Kans. Acad. Sci.* **60**, 419–424.
Mukinya, J. G. (1973). Density, distribution, population structure and social organisation of the black rhinoceros in Masai Mara Game Reserve. *E. Afr. Wildl. J.* **11**, 385–400.
Mukinya, J. G. (1977). Feeding and drinking habits of the black rhinoceros in Masai Mara Game Reserve. *E. Afr. Wildl. J.* **15** (2), 125–138.
Noack, T. (1893). Das Quagga. *Zool. Gart. Frankfurt* 34, 289–297.
Nobis, G. (1955). Beiträge zur Abstammung and Domestikation des Hauspferdes. *Z. f. Tierzücht, u. Züchtungsbiol.* **64**, 201–246.
Norris, T. (1976). "Report to East African Wildlife Society." *Africana*, **6**.
Osborn, H. F. (1918). Equidae of Oligocene, Miocene and Pliocene. *Mem. Amer. Mus. Nat. Hist.* **1918**.
Osterhoff, D. R. and Keep, M. E. (1970). Natural variation in the blood proteins of white and black rhinoceros. *Lammergeyer* **11**.
Ottaway, C. W. (1961). Aspects of equine and canine locomotion. *In* "Vertebrate Locomotion." Symp. Zool. Soc. London No. 5 (Harris, J. E. ed.), pp. 101–113, Academic Press. London and New York.
Owaga, M. L. A. (1975). Feeding ecology of wildebeest and zebra in Athi-Kaputei Plains. *E. Afr. Wildl. J.* **13**, (3, 4), 375.
Owaga, M. L. A. (1977). Comparison of analysis of stomach contents and faecal samples from zebra. *E. Afr. Wildl. J.* **15** (3), 217–222.
Owen, T. R. H. (1956). The black and white rhinoceroses. *Uganda Wildlife and Sport*. **1**, 27–31.
Owen-Smith, N. (1971a). Territoriality: the example of the white rhinoceros. *Roneoed Pap. Anim. Beh. Symp. Zool. Soc. S. Afr.*
Owen-Smith, N. (1971b). Territoriality in the white rhinoceros, *Ceratotherium simum* Burchell. *Nature, London* **231**, 294–296.
Owen-Smith, N. (1972). The contribution of radiotelemetry to a study of the white rhinoceros. Symp. on Biotelem. Pretoria 1971 CSIR Pretoria.
Owen-Smith, N. (1974). The social system of the white rhinoceros. *In* "The Behaviour of Ungulates and its Relation to Management." (Geist, V. and Walther, F. eds.), IUCN Publication No. 24.
Owen-Smith, N. (1975). The social ethology of the white rhinoceros *Ceratotherium simum* (Burchell 1817). *Z. Tierpsychol.* **38**, 337–384.
Parsons, B. T. and Sheldrick, D. L. W. (1964). Some observations on biting

flies (*Diptera Muscidae*, *Stomoxydinae*), associated with the black rhinoceros, *Diceros bicornis* L. *E. Afr. Wildl. J.* **2**, 77–85.
Patterson, B. (1966). A new locality for early Pleistocene fossils in Northwestern Kenya. *Nature, London* **212**, 577–581.
Patterson, B., Behrensmeyer, A. K. and Sill, W. D. (1970). Geology and fauna of a new Pliocene locality in North-Western Kenya. *Nature, London* **226**, 918–921.
Percival, A. B. (1928). "A Game Ranger on Safari." London.
Peterson, J. C. B. and Casebeer, R. K. (1972). Distribution, population status and group composition of wildebeest, *Connochaetes taurinus*, and zebra, Equus burchelli, on the Athi-Kapiti plains Kenya. *Project Working Document* 2. Wildlife Management Project in Kenya FAO of the University Nairobi.
Pienaar, U. de V. (1970). The recolonisation history of the square-lipped rhinoceros, *Ceratotherium simum simum* Burchell in the Kruger National Park. *Koedoe* **13**, 157–169.
Pitman, C. R. S. (1927). Annual Report of the Game Department. Government Printer, Entebbe, Uganda.
Pitman, C. R. S. (1950). Annual Report of the Game Department. Government Printer, Entebbe, Uganda.
Pitman, C. R. S. (1956). Weapons of the two African rhinoceroses. *Oryx* **3**, 195–196.
Player, I. C. (1967). Translocation of white rhinoceros in South Africa. Oryx **19** (2), 137–150.
Player, I. C. and Feely, J. M. (1960). A preliminary report on the square-lipped rhino, *Ceratotherium simum simum. Lammergeyer* **1**, 3–25.
Pocock, R. I. (1897). The species and subspecies of zebra. *Ann. Mag. Nat. Hist. London* **6** (20), 33–52.
Pocock, R. I. (1902). A new arrangement of the existing species of *Equidae* with the description of a new subspecies of zebra. *Ann. Mag. Nat. Hist. London* **7** (10), 304–308.
Pocock, R. I. (1903). The coloration of the quaggas. *Nature, London* **68**, 356–357.
Pocock, R. I. (1904). The Cape Colony Quaggas. *Ann. Mag. Nat. Hist. London* **7** (14), 313–328.
Pocock, R. I. (1909a). On the colours of horses, zebras and tapirs. *Ann. Mag. Nat. Hist. London* **8** (4), 404–415.
Pocock, R. I. (1909b). Photographs of Burchell's and Wahlberg's quaggas. *Proc. Zool. Soc. London* 415–419.
Portman, A. (1952). "Animal Forms and Patterns." Faber and Faber, London.
Potter, H. B. (1949). Rhino as we know them. *Afr. Wildlife* **3**, 128–138.
Potter, H. B. and Mitchell, D. C. (1947). Rhino black or white. *Field, London* **190**, 384–385.
Quinn, H. J. (1955). Miocene Equidae of the Texas Gulf coastal plain. University of Texas Publication No. 5516, p. 102.
Quinn, H. J. (1957). Pleistocene Equidae of Texas. University of Texas Rep. of Invest. 33, p. 51.

Radinsky, L. B. (1969). The early evolution of the Perissodactyla. *Evolution, Lancaster* **23**, 308–328.

Richards, D. (1972). Square-lipped rhinoceros behaviour. *Lammergeyer* **15**.

Ridewood, W. G. (1901). On the hairs of *Equus burchelli* and *Equus zebra*. *Proc. Zool. Soc. London* **1**, 87.

Ridgeway, W. (1909). Contributions to the study of the *Equidae*, I. The differentiation of the three species of zebras. II On hitherto unrecorded specimens of *Equus quagga*. *Proc. Zool. Soc. London* **1909**, 547–588.

Ripley, S. D. (1952). Territorial and sexual behaviour in the great Indian rhinoceros, a speculation. *Ecology New York* **33**, 570–573.

Ripley, S. D. (1958). Comments on the black and square-lipped rhinoceros species in Africa. *Ecology New York* **37** (1), 172–174.

Ritchie, A. T. A. (1963). The black rhinoceros *Diceros bicornis* L. *E. Afr. Wildl. J.* **1**, 54–62.

Robb, R. C. (1935). A study of mutations in evolution. Part I, Evolution of the Equine skull. Part II, Ontogeny of the Equine skull. *J. Genetics* **31**, 39–52.

Roth, H. H. and Child, G. (1968). Distribution and population structure of the black rhinoceros, *Diceros bicornis* L., in the Lake Kariba basin. *Z. Säugetierk.* 33, 214–226.

Round, H. C. (1964). A new species of *Stephanofilaria* in skin lesions from the black rhinoceros, *Diceros bicornis* L., in Kenya. *J. Helminth.* **38**, 87–96.

Ryden, H. (1970). "America's last Wild Horses." Dutton, New York.

Ryder, M. L. (1962). Structure of rhinoceros horn. *Nature, London* **193**.

Rzasnicki, A. (1936). Zur Kenntniss und Entdeckungsgeschichte des Grevy-Zebras. *Zool. Gart. Leipzig* **8**, 283–291.

Rzasnicki, A. (1951). Zebras and Quaggas. *Ann. Mus. Zool. Pol. XIV Warszawa* **16**, 203–245.

Savidge, J. M. (1964). Second introduction of white rhino into the Murchison Falls National Park Uganda. Mimeograph 6 pp.

Schaller, G. B. (1972). "The Serengeti Lion: a study of predator-prey relations." University of Chicago Press, U.S.A.

Schaller, G. B. (1973). "Golden Shadows, Flying Hooves." A. Knopf, New York.

Schaurte, W. T. (1960). Vom Breitmaul-Nashorn. *Natur u. Volk* **90**, 389–397.

Schaurte, W. T. (1969). Über die Geburt eines Breitmaul-Nashörnes, *Ceratotherium simum*, in Wildschutzgebiet Krugersdorp in Transvaal. *Saugetierk. Mitt.* **17**, 158–160.

Schenkel, R. (1966). Zum Problem der Territorialität und des Markierens beim Säugern—am Beispiel des Schwarzen-Nashorns und des Löwens. *Z. Tierpsychol.* **23** (5), 593–626.

Schenkel, R. and Lang, E. M. (1969). Das Verhalten der Nashörner. *Handb. Zool.* **8**, 10.

Schenkel, R. and Schenkel-Hulliger, L. (1969). Ecology and behaviour of the black rhinoceros (*Diceros bicornis* L.), a field study. *In* "Mammalia Depicta," Verlag Paul Parey, Hamburg and Berlin.

Schloeth, R. (1958). Das Scharren bei Rind und Pferd. *Z. Säugetierk.* **23**, 139–147.
Schneider, K. M. (1930). "Das Flehmen." Leipzig.
Schultz, K. C. A. and Kluge, E. B. (1960). Dernatitis in the black rhinoceros *Diceros bicornis* due to filariasis. *S. Afr. Vet. Med. Ass.* **31**, 265–269.
Selous, F. C. (1881). "On the South African Rhinoceroses." *Proc. Zool. Soc. London* **1881**.
Sheldrick, K. (1975). Black rhinoceros with supernumary horns. *Africana* **5** (11).
Sidney, J. (1965). The past and present distribution of some African ungulates. *Trans. Zool. Soc. London* **30**, 5–397.
Simpson, G. G. (1951). "Horses." Oxford University Press, Oxford.
Skoog, R. O. and Kogan, P. J. (1975). The plains zebra (*Equus burchelli boehmi* matschie) of East Africa: its status and role in Man's development of the tropical savanna. Serengeti Project 33. Texas A. M. University Programme in Ecology, U.S.A.
Slijper, E. J. (1946). The vertebral column and spinal musculature of mammals. *Verh. Akad. Wet. Amsterdam* **42**, 5.
Smith, J. M. and Savage, R. J. G. (1955). Locomotory adaptations in mammals. *J. Linn. Soc. Zool.* **42**, 603–622.
Smuts, E. L. (1975). Home range sizes for Burchell's zebra. *Equus burchelli antiquorum* from the Kruger National Park. *Koedoe* **18**, 139–146.
Sody, H. V. (1959). Das Javanisch Nashorn *Rhinoceros sondaicus*. *Z. Säugetierk.* **24**, 109–240.
Sokal, R. R. (1966). Numerical taxonomy. *Scient. Amer.* 215, (Dec.).
Sondaar, P. Y. (1961). Les Hipparions de l'Aragon méridional. *Estudios Geologicos* **17**, 209–305.
Sondaar, P. Y. (1969). Some remarks on horse evolution and classification. *Z. Säugetierk.* **34**, 307–311.
Spinage, C. A. (1961). Some notes on the rhinoceros. *Afr. Wildlife* **14**, 95–100.
Spinage, C. A. (1962). "Animals of East Africa." Collins, London.
Spinage, C. A. (1972). Age estimation of zebra. *E. Afr. Wildl. J.* **10** (4), 273–277.
Spinage, C. A. and Guinness, F. E. (1972). Effects of fire in the Akagera National Park and Mutara Hunting Reserve Rwanda. *Rev. Zool. Bot. Afr.* **56** (3–4), 302–336.
Spinage, C. A., Guinness, F., Eltringham, S. K. and Woodford, M. H. (1972). Estimation of large mammal numbers in the Akagera National Park and Mutara Hunting Reserve Rwanda. *Terre et Vie* **4**, 561–570.
St Croix, O. H. de (1962). The white rhinos of Hluhluwe. *J. Bombay Nat. Hist. Sci.* **58**, 231–333.
Stewart, D. R. M. and Stewart, J. (1963). The distribution of some large mammals in Kenya. *J. E. Afr. Nat. Hist. Soc.* **24** (3), 8.
Stirton, R. A. (1940). Phylogeny of North America Equidae. *University California Publ. Bull. Dept. Zool. Sci.* **21**, 165–198.
Stirton, R. A. (1942). Comments on the origin and generic status of *Equus*. *J. Paleont.* **16**, 627–637.

St Leger, J. (1932). On *Equus quagga* of South-West and East Africa. *Ann. Mag. Nat. Hist.* **10**.

Stockley, C. H. (1950). The hook-lipped rhino. *Zoo Life London* **5**, 88–91.

Stubbs, G. (1965). "The Anatomy of the Horse." (Original 1766 ed. and illustr. with modern Vet, paraphrase by J. McCann.) J. A. Allen & Co., London.

Sutherst, R. W. (1964). Now Kenya saves its rhinos. *Animals* **4**, 215.

Swynnerton, G. H. (1959). Threat to black rhino in East Africa. *Wildlife Nairobi* **1** (1), 14–16.

Talbot, L. M. (1960). A look at threatened species. A report on some animals of the Middle East and Southern Asia which are threatened with extermination. *Oryx* **5**, 153–293.

Teilhard, de Chardin, P. (1936). Fossil mammals from locality 9 of Choukoutien. *Palaeont. Sin.* C **7**, 1–61.

Teilhard, de Chardin, P. and Piveteau, J. (1930). Les mammifères fossiles de Nihowan (Chine). *Ann. Paléont. Paris.* **19**, 1–134.

Thenius, E. (1955a). Zur Kenntniss der Unter-Pliozänen *Diceros* Arten. *Ann. Natur. Mus. Wien* **60**, 202–211.

Thenius, E. (1955b). Die Verknöcherung der Nasenscheidewand bei Rhinocerotiden. *Mém. Suisse Paléont.* **71** (4), 1–17.

Thenius, E. and Hofer, H. (1960). "Stammesgeschichte der Säugetiere." Berlin, Göthingen, Heidelberg.

Tindell-Hopwood, A. (1937). Contributions to the study of some African mammals. II The subspecies of the black rhinoceros *Diceros bicornis* Linn. defined by the proportions of the skull. *J. Linn. Soc. Zool.* **40**, 447–457.

T. P. R. (1961). Tanzania National Park Reports.

Tremlett, J. G. (1961). Unpublished report on the examination of three rhinoceroses from The Tsavo National Park (East) Kenya.

Tremlett, J. G. (1964). Observations on the pathology of lesions associated with *Stephanofilaria dinniki* from the black rhinoceros *Diceros bicornis*. *J. Helminth.* **38**, 171–174.

Trumler, E. (1958). Boebachtungen an den Böhmzebras des Georg-von-Opel-Freigeheges für Tierforschung I Das Paarungsverhalten. *Säugetierk. Mitt.* **6**, 1–48.

Trumler, E. (1959). Das "Rossigkeitgesicht" und ähnliches Ausdrucksverhalten bei Einhufern. *Z. Tierpsychol.* **16**, 478–488.

Trumler, E. (1961). Entwurf einer Systematik der rezenten Equiden und ihre fossilen Verwandten. *Säugetierk Mitt.* **9**, 109–125.

Tyler, S. J. (1968). The social life of the New Forest ponies. *Animals* **11**, 145–147.

Tyler, S. J. (1969). The behaviour and social organisation of the New Forest ponies. Dissertation, Cambridge.

Tyler, S. J. (1972). The behaviour and social organisation of New Forest ponies. *An. Behav. Mon.* **5** (2).

UGR (1928). Annual Report of Game Department Uganda for 1928.

Ullrich, W. (1964). Zur Biologie der Panzernashörner (*Rhinoceros unicornis*) in Assam. *D. Zool. Gart (NF)* **28**, 225–250.

Ulmer, F. A. (1941). The living Rhinoceros. *Fauna* **3** (1), 3–10.

Vaughan-Kirby, F. (1920). The white rhinoceros with special reference to its habit in Zululand. *Ann. Durban Mus.* **2**, 223–242.

Verheyen, R. (1951). "Contribution à l'étude éthologique des mammifères du Parc National de L'Upemba." Inst. Parcs Nat. Congo Belge, Brussels.

Vesey-Fitzgerald, D. F. (1960). Grazing succession among East African game animals. *J. Mammal.* **4**, 161–172.

Vesey-Fitzgerald, D. F. (1965). The utilization of natural pastures by wild animals in the Rukwa Valley Tanganyika. *E. Afr. Wildl. J.* **3**, 38–48.

Vincent, J. (1961). The status of square-lipped rhinoceros, *Ceratotherium* simum simum in Zululand. *Lammergeyer* **10**, 12–21.

Vincent, J. (1974). The management of large mammals in Natal, with special reference to utilization for stocking or restocking purposes. *In* "The Behaviour of Ungulates and its Relation to Management." (Geist, V. and Walther, F. eds.), IUCN Publication No. 24, 1974.

Wackernagel, H. (1964a). Grant's zebra *Equus burchelli boehmi* at Basle Zoo, a contribution to breeding biology. *Int. Zoo. Yearbook* **5**, 38.

Wackernagel, H. (1964b). Die Basler Grant-Zebra-Gruppe. *Bull. Zool. Gart. Basel*, 12–13.

Walther, F. (1961). On the mother/young relationship and the role of the stallion in rearing a zebra foal, *Equus quagga boehmi. Yhrb. Operg. and Opel Zoo* **3**, 116–128.

Watson, J. M. (1949). The wild animals of Teso and Karamoja, Uganda. *Uganda J.* **13** (2), 182–201.

Western, D. and Sindiyo, D. M. (1972). The status of the Amboseli rhino population. *E. Afr. Wildl. J.* **10**, 43–57.

Willemse, M. C. A. (1950). The shifting of the molar row with regard to the orbit in Equus and Giraffe. *Zool.* Medl. **30**, 23.

Williams, M. (1956). "Horse Psychology." Methuen, London.

Willoughby, D. P. (1946). The zebra is a dark horse. *Fauna Philadelphia* **8** (3), 67–70.

Willoughby, D. P. (1966). The vanished quagga. *Natural History* **75** (2), 60–63.

Willoughby, D. P. (1974). "The Empire of Equus." South Brunswick and New York.

Wilson, V. J. and Edwards, P. W. (1965). Data from a female rhinoceros and foetus *Diceros bicornis* Linn. from the Fort Jameson district. *Puku* **3**, 179–180.

Wood, H. E. (1949). Evolutionary rates and trends in rhinoceros. *In* "Genetics, Palaeontology and Evolution." (Jepson, Mayr and Simpson eds), pp. 185–189. Princetown, New Jersey.

Wyman, W. D. (1945). "The Wild Horse of the West." University of Nebraska Press.

Wynne-Edwards, V. C. (1962). "Animal Dispersion in Relation to Social Behaviour." Oliver and Boyd, Edinburgh.

Zdansky, O. (1928). Die Säugetiere der Quartärfauna von Chou-Kou-Tien. *Palaeont. Sin.* C **5**, 1–146.

Zdansky, O. (1935). *Equus* und andere Perissodactyla. *Paleont. Sin.* C **6**, 1–54.

Zeeb, K. (1958). Paarungsverhalten bei Primitivpferden. *Säugetierk Mitt.* **6**, 51–59.
Zeeb, K. (1959). Verhaltensforschung beim Pferd. *Tierärztl. Umsuch.* **14** (1), 334–341.
Zeeb, K. (1961). Der Freie Herdensprung bei Pferden. *Wien Tierärtzl. Msch.* **48**, 90–102.
Zeeb, K. (1965). "Wildpferde in Dülmen." Verlag Halwag Bern.
Zukowsky, L. (1922). Vorläufige Mitteilung über eine neue Art des Spitzschnauz-Nashorns aus Südwest-Afrika. *Arch. Naturgesch.* A **88** (7–12), 162–163.
Zukowsky, L. (1949). Eine neue Nashornrasse aus dem Schari-Tschad Gebiet. *Arch. Noah* **1**, 16.
Zukowsky, L. (1964a). Die Systematik der Gattung *Diceros* Gray 1821. *Zool. Gart. Leipzig* **30**, 1–104.
Zukowsky, L. (1964b). Ridiculous splitting of rhinos. *Zool. Gart. Leipzig* **30**, 1–104.
Zumpt, F. (1964). Parasites of the white and black rhinoceros. *Lammergeyer* **3** (1), 59–70.

Non-Bovid Artiodactyls

Allen, G. M. (1939). A checklist of African mammals. *Bull. Mus. Comp. Zool. Harvard* **83**, 1–763.
Amoroso, E. C., Edholm, O. G. and Rewell, R. E. (1947). Venous valves in the giraffe, okapi, camel and ostrich. *Proc. Zool. Soc. London* **117**, 435–440.
Anderson, J. (1912). "Zoology of Egypt." London.
Angemeyer, M. (1966). Zur Kenntniss der Halsmuskeln und Halsnerven von *Giraffa camelopardalis*. *Zool. Anz.* **177**, 188–201.
Annison, E. F. and Lewis, D. (1959). "Metabolism in the Rumen." Methuen, London.
Ansell, W. F. H. (1964). Addenda and corrigenda to "Mammals of Northern Rhodesia" No. 1, *Puku Occ. Papers*, **2**, 14–52.
Ansell, W. F. H. (1965). Feeding habits of *Hippopotamus amphibius* Linn. *Puku* **3**, 171.
Ansell, W. F. H. (1968). Artiodactyla. *In* "Preliminary Identification Manual for African Mammals." (Meester, J. ed.) Smithsonian Institution, Washington.
Ansell, W. F. H. and Dagg, A. I. (1971). The scientific name of the reticulated giraffe. *Bull. Zool. Nomencl.* **28** (3–4).
Anthony, R. and Coupin, F. (1925). Recherches anatomiques sur l'Okapi, *Okapia johnstoni*. *Acl. Rev. Zool. Afr.* **13**, 69–96.
Arambourg, C. (1933). Mammifères Miocènes du Tukana. *Ann. Paléont.* **22**, 123–146, Paris.
Arambourg, C. (1943). Observations sur les suidès fossiles du Pléistocène d'Afrique. *Bull. Mus. Hist. Nat.* **2** (15), 471–476.
Arambourg, C. (1944). Les Hippopotames fossiles de l'Afrique. *C.R. Hebd. Séanc. Acad. Sci. Paris* **218**, 602–604.

Arambourg, C. (1945). Au sujet de *l'Hippopotamus hipponensis* Gaudry. *Bull. Soc. Géol. Fr.* **14** (5), 147–153.
Arambourg, C. (1947–48). Contribution à l'étude géologique et paléontologique du bassin du Lac Rudolphe et de la basse Vallée de l'Omo, I et II. *Miss. Scient. Omo*, **1** (3), 231–562.
Arambourg, C. (1948). Un Sivatherium Nordafricain, *Libytherium maurasium* Pomel. *C.R. Soc. Géol. Fr.* (5), 178.
Arambourg, C. (1961). Note préliminaire sur quelques vertébrés nouveaux du Burdigaline de Libye. *C.R. Somm. Géol. Fr.* 107–108.
Arambourg, C. (1963). Le genre *Bunolistriodon* Arambourg 1933. *Bull. Soc. Géol. Fr.* **5** (7), 903–911.
Arambourg, C., Chavaillon, J. and Coppens, Y. (1967). Premiers résultats de la nouvelle mission de l'Omo 1967. *C.R. Hebd. Séanc. Acad. Sci. Paris* **265**, 1891–1896.
Arambourg, C., Chavaillon, J. and Coppens, Y. (1969). Résultats de la nouvelle mission de l'Omo. *C.R. Hebd. Séanc. Acad. Sci. Paris* D **268**, 759–762.
Arman, P. and Field, C. R. (1973). Digestion in the hippopotamus. *E. Afr. Wildl. J.* **11** (1).
Arnold, R. (1949). Eine ungefleckte Giraffe in Nord-Ost Africa. *Z. Säugetierk.* **15**, 306–311.
Attwell, R. I. G. (1963). Surveying Langwa hippo. *Puku Occ. Papers* 29–50.
Azzaroli, A. (1954). Filogenesi e biologia di *Sus strozzi* e di *Sus minor*. *Paleontografia Italica* **48**, 41–76, Pisa.
Babault (1949). Notes: éthologiques sur quelques mammifères africains. *Mammalia* **13**, 57–58.
Backhaus, D. (1960a). Pragung einer Giraffe auf den Menschen? *Säugetierk Mitt.* **8**, 29–31.
Backhaus, D. (1960b). Pragung auch bei Giraffen? *Natuwiss.* **47**, 118.
Backhaus, D. (1961). "Beobachtungen an Giraffen in zoologischen Garten und freier Wildbahn." pp. 1–202. Brussels Inst. Parcs Nationaux du Congo et du Ruanda Urundi.
Baker, S. W. (1872). "The Nile Tributaries of Abyssynia and the Sword Hunters of the Hamran Arabs." MacMillan and Co. London.
Bate, D. M. A. (1934). A fossil warthog from Palestine. *Ann. Mag. Nat. Hist. London* **13** (10), 120–129.
Beaton, W. K. (1947). Notes from the Nairobi National Parks. *Nature in East Africa* 3, 14–15.
Beaufort, L. de (1928). On a case of correlation between blood vessels and colour pattern in a giraffe. *Tijdschr. Nederl. Dierk. Ver.* 3 (1), 31.
Beaux, O. de (1924). Beitrag zur Kenntniss der Gattung *Potamochoerus* Gray. *Zool. Yahrb.* **47**, 379–504.
Belt, T. (1874). "The Naturalist in Nicaragua." London.
Bemmel, A. C. van (1959). The new okapi house at the Rotterdam Zoo. *Nether. Int. Zoo Yearbook* **1**, 38–39.
Bere, R. M. (1959). The hippopotamus problem and experiment. *Oryx* **5** (3), 116–124.
Bergh, L. van den and Boué, G. (1945). De la parenté sérologique de l'okapi et de la girafe. *Bull. Acad. Belg. Sci.* **30**, 239–244.

Berlin, W. (1858). Ist der Magen von *Moscus javanicus* wesentlich von dem anderer Wiederkäuer verschieden? *Arch. Holländ. Beitr. Natur. u. Heilk.* **1**, 471–476.

Berry, P. S. M. (1978). Range movements of giraffe in the Luangwa Valley, Zambia. *E. Afr. Wildl. J.* **16** (2).

Best, G. A. (1962). "Records of Big Game." 11th Ed. Rowland Ward, London and Nairobi.

Bigalke, R. (1951). The discovery of the giraffe in South Africa. *Fauna and Flora Pretoria* **2**.

Bigourdan, J. (1948). Le Phacochère et les Suidés dans l'Ouest africain. *Bull. Inst. Fr. Afr. Noire* **10**, 285–360.

Bishop, W. W. (1958). Miocene mammalia from the Napak Volcano, Karamoja, Uganda. *Nature, London* **182**, 1480–1482.

Bishop, W. W. (1963). The later Tertiary and Pleistocene in Eastern Equatorial Africa. *In* "African Ecology and Human Evolution." (Howell, F. C. and Bourlière, F. eds.), *Viking Fund Publications in Anthropology* No. 36, New York.

Bishop, W. W. and Whyte, F. (1962). Tertiary mammalian fauna and sediments in Karamoja and Kavirondo East Africa. *Nature, London* **196**, 1283–1287.

Blancou, L. (1963). A propos de la distribution de la Girafe en Afrique. *Mammalia* **27**, 311–312.

Blankenship, L. H. and Field, C. R. (1972). Factors affecting the distribution of wild ungulates on a ranch in Kenya. Prelim. report *Zool. Africana* **7**, 281–302.

Block, W. (1968). Ticks from waterbuck and warthog in Queen Elizabeth National Park Uganda. *E. Afr. Wildl. J.* **6**, 140–141.

Boas, J. E. V. (1890). Zur Morphologie des Magens der Cameliden und der Traguliden und über die systematische Stellung letzerer Abteilung. *Morph. Jahrb.* **16**, 494–524.

Bohlin, B. (1926). Die Familie Giraffidae. *Paleont. Sin.* (C) **4**, Peking.

Bohlken, H. (1960). Remarks on the stomach and the systematic position of the Tylopoda. *Proc. Zool. Soc. London* **134**, 207–215.

Bolton, M. (1973). Notes on the current status and distribution of some large mammals in Ethiopia. *Mammalia* **37** (4), 562–585.

Bouchud, J. (1966). Le genre *Hippopotamus*. *In* "Faunes et Flores pre-historiques de l'Europe occidentale." (Lavocat, R. ed.) pp. 216–244. Boubée et Cie, Paris.

Bourdelle, M. E. (1934). Les allures de la girafe en particulier le galop. *Bull. Mus. Hist. Nat.* **2** (6), 4, 329–339.

Bourlière, F. (1955). "The Natural History of Mammals." G. Harrap, London.

Bourlière, F. (1961). Le sex ratio de la girafe. *Mammalia* **25**, 467–471.

Bourlière, F. (1962). The uniqueness of the African big-game fauna. *Afr. Wildlife* **16** (2), 95–100.

Bourlière, F. (1963). Observations on the ecology of some large African mammals. *In* "African Ecology and Human Evolution." (Howell, F. C. and Bourlière, F. eds.), Viking Fund Publications No. 36, New York.

Bourlière, F. (1965). Ecological notes on the Tsavo. *Afr. Wildlife* **19**, 47–107.
Bourlière F. and Verschuren, J. (1960). Introduction à l'écologie des Ongulés du Parc National Albert. *Éxplorat Parcs Natn. Albert*, Inst. Parcs Natn. Congo Belge, Brussels.
Bradley, R. M. (1968). Some aspects of the ecology of the warthog. M.Sc. thesis University of East Africa.
Bradley, R. M. (1971). Warthog (*Phacochoerus aethiopicus*) Pallas burrows in Nairobi National Park. *E. Afr. Wildl. J.* **9**, 149–152.
Bradley, R. M. (1972). A photographic ageing technique used on warthog. *E. Afr. Wildl. J.* **10** (2), 123–128.
Bramachary, R. L. (1971a). A note on the food habits of the giraffe in East Africa. *Uganda J.* 33, 214–216.
Bramachary, R. L. (1971b). An additional note on the food habits of the giraffe in East Africa. *Uganda J.* 33, 1971.
Bramachary, R. L. (No date). A note on the food habits of giraffe in altered habitats. (Mimeo. Report).
Breytenbach, G. J. and Skinner, J. D. (in press). The ecology of bushpigs, *Potamochoerus porcus* Linn. on the eastern shores of Lake St. Lucia. Pretoria University.
Brooks, A. C. (1960). Notes on Queen Elizabeth Park hippo experiments. Uganda Game Dept. Committee.
Brooks, A. C. (1961). Some notes on the Acholi/East Madi elephant sanctuary and sleeping sickness area. (Mimeo.) Uganda Game Dept. Entebbe.
Broom, R. (1925). On evidence of a giant pig from the late Tertiaries of South Africa. *Rec. Albany Mus.* 3, 307–308.
Brown, F. (1947). Giraffe Noises. *Field, London* **189**, 76.
Brown, W. L. (1960). Ants, Acacias and browsing animals. *Ecology* **41**, 587–592.
Brownlee, A. (1962). Evolution of the giraffe. *Nature, London* **200**, 1022.
Brückner, R. (1950). Das Auge des Okapi. *Acta Tropica Basel* **7**, 188–192.
Bruhin, H. (1950). Okapi Bibliographie. *Acta Tropica Basel* **7**.
Buck, A. C., Leivestad, H., Meya, A., Nganwa-Baguma, A. B., Nkugwa, J., Rayner, D. V., Richardson, H. D., Tejani, D. and Wright, P. G. (1969). Some observations on the blood of the hippopotamus (*Hippopotamus amphibius*). *Makerere Med. J.* **13**, 25–28.
Burton, M. (1953). Water chevrotains. *Ill. Lond. News* **223**, 746.
Burton, M. (1954). The colours of the river horse. *Ill. Lond. News* **224**, 672–673.
Burtt, B. D. R. (1929). A record of fruits and seeds dispersed by mammals and birds from the Singida district of Tanganyika Territory. *J. Ecol.* **17** (2), 351–355.
Carlsson, A. (1926). Über die Tragulidae und ihre Beziehungen zu den übrigen Artiodactylen. *Acta Zoologica* **69**.
Causey-Whittow, G. (1976). The mouse-deer of Malaya's forests. *Wildlife* **18**, 12 Dec.
Cave, A. J. E. (1950). On the liver and gall bladder of the giraffe. *Proc. Zool. Soc. London* **120**, 381.

Cena, K. (1964). Thermoregulation in the hippopotamus. *Int. J. Biometr.* **8**, 57–60.
Chardin, T. de and Trassaert, M. (1937). The Pliocene Camelidae, Giraffidae and Cervidae of Southeastern Shansi. *Paléont. Sin. (NF)* C **1**.
Charnot, Y. (1963). The development of the soft palate and physiological states in the dromedary. *J. Physiol. Paris* **55**, 226–227.
Child, G. (1962). Hippo hunt in the Sahara. *Afr. Wildlife* **16**, 337–339.
Child, G. (1968). "Behaviour of Large Mammals During the Formation of Lake Kariba. Nat. Mus. Rhodesia. Salisbury.
Child, G., Sowls, L. and Mitchell, B. L. (1965). Variations in the dentition, ageing criteria and growth patterns in warthog. *Arnoldia Rhodesia* **1** (38), 1–23.
Child, G., Roth, H. H. and Kerr, M. (1968). Reproduction and recruitment patterns in warthog (*Phacochoerus aethiopicus*) populations. *Mammalia* **32** (1), 6–29.
Christy, C. (1924). African forests, bush and buffaloes. *Bull. Zool. Soc. N. Y.* **27**, 130–142.
Citters, R. L. van, Kemper, W. S. and Franklin, D. L. (1966). Blood pressure responses of wild giraffes studied by radio telemetry. *Science* **152**, 384–386.
Clark, W. E. le Gros (1939). The brain of the okapi. *Proc. Zool. Soc. London* **109**, 153–159.
Clarke, J. R. (1953). The hippopotamus in Gambia West Africa. *J. Mammal.* **34**, 299–315.
Clough, G. (1966). Reproduction in the hippopotamus, *Hippopotamus amphibius* Linn. PhD. thesis University of Cambridge.
Clough, G. (1969). Some preliminary observations on reproduction in the warthog (*Phacochoerus aethiopicus*) Pallas. *J. Reprod. Fert. Suppl.* **6**, 323–327.
Clough, G. (1970). A record of "testis cords" in the ovary of a mature hippopotamus (Hippopotamus amphibius) Linn. *Anat. Rec.* **166**, 47–50.
Clough, G. and Hassam, A. G. (1970). A quantitative study of the daily activity of the warthog in the Queen Elizabeth National Park Uganda. *E. Afr. Wildl. J.* **8**, 19–24.
Cobb, S. (1976). The distribution and abundance of the large herbivore community of Tsavo National Park Kenya. D.Phil. thesis, Oxford University.
Coe, M. J. (1967). "Necking" behaviour in the giraffe. *J. Zool.* **151**, 313–321.
Colbert, E. H. (1935a). The phylogeny of the Indian Suidae and the origin of the Hippopotamidae. *Amer. Mus. Novit. New York* **799**, 1–24.
Colbert, E. H. (1935b). The classification and the phylogeny of the Giraffidae. *Amer. Mus. Novit. New York* **800**, 1–15.
Colbert, E. H. (1936). Was the extinct giraffe, *Sivatherium*, known to early Sumerians? *Amer. Anthrop.* **38**, 605–608.
Colbert, E. H. (1938). The relationship of the Okapi. *J. Mammal.* **19**, 47–64.
Cooke, H. B. S. (1949). The fossil Suina of South Africa. *Trans. R. Soc. S. Afr.* **32**, 1–44.
Cooke, H. B. S. (1974). The fossil mammals of Cornelia. *S. Afr. Nat. Mus. Bloemfontain Mem.* **9**.

Cooke, H. B. S. (in press). The pliocene-Pleistocene Suidae of Africa.
Cooke, H. B. S. and Coryndon, S. C. (1970). Pleistocene mammals from the Kaiso formation and other related deposits in Uganda. *In* "Fossil Vertebrates of Africa" Vol. 2 (Leakey, L. S. B. and Savage, R. J. G. eds), pp. 107–224. Academic Press, London and New York.
Cooke, H. B. S. and Ewer, R. F. (1972). Fossil Suidae from Kanapoi and Lothagam Northwestern Kenya. *Bull. Mus. Comp. Zool. Harvard* **143** (3), 149–295.
Cooke, H. B. S. and Maglio, V. J. (1972). Plio-Pleistocene stratigraphy in East Africa in relation to proboscidean and suid evolution. *In* "Calibration of Hominid Evolution." Wenner Gren Foundation.
Cooke, H. B. S. and Wells, L. (1947). Fossil mammals from the Makapas Valley Potgietersrut. 3, Giraffidae. *S. Afr. J. Sci.* **43**, 232.
Copley, H. (1949). The pigs of Kenya. *Nature in East Africa* **2** (2), 6–10.
Corbet, G. B. (1969). The taxonomic status of the pigmy hippopotamus *Choeropsis liberiensis* from the Niger delta. *J. Zool. London* **158**, 387–394.
Cordier, J. A. (1893). Observations d'anatomie comparée sur l'estomac des Caméliens. *Bull. Soc. Zool. France* **18**, 75–78.
Coryndon, S. C. (1967). Hexaprotodont Hippopotamidae of East Africa and the phylogeny of the family. *Extrait Congrés Panafricain de Prehistoire Dakar*, **1967**.
Coryndon, S. C. (1970). The extent of variation in fossil *Hippopotamus* from Africa. *In* "Variations in Mammalian Populations" Symp. Zool. Soc. London, No. 26 (Berry, R. J. and Southern, H. N. eds.), pp. 135–147. Academic Press, London and New York.
Coryndon, S. C. (1973). Fossil Hippopotamidae from Pliocene/Pleistocene successions of the Rudolph basin. Paper for Conf. Stratigraphy Palaeontology and Evolution. Wenner Grenn Foundation (not for publication).
Coryndon, S. C. (in press). Fossil Hippopotamidae of Africa.
Coryndon, S. C. and Coppens, Y. (1973). Preliminary report on Hippopotamidae (Mammalia, Artiodactyla) from the Plio-Pleistocene of the lower Omo basin Ethiopia. *In* "Fossil Vertebrates of Africa" Vol. 3, (Leakey, L. S. B., Savage, R. J. G. and Coryndon, S. C. eds), pp. 139–157. Academic Press, London and New York.
Crawford, M. A., Gale, M. M. and Woodford, M. H. (1969). The polyenoic acids and their elongation products in the muscle tissue of *Phacochoerus aethiopicus*: a revaluation of animal fat. *Biochem. J.* **113**, 27.
Crisp, E. (1867). On some points connected with the anatomy of the hippopotamus, *H. amphibius*. *Proc. Zool. Soc.* London, 601–612.
Crusafont, P. (1952). Los girafidos fosiles de España. *Mem. Inst. Geol.* **8**, Barcelona.
Crusafont, P. (1958). Nouvelle vue sur la classification paléontologique des *Pecora*. *Mammalia* **22**, 45–52.
Cumming, D. H. M. (1970). A contribution to the biology of warthog, *Phacochoerus africanus* Gmelin in the Sengwa Region of Rhodesia. PhD. Dissertation Rhodes University.
Cumming, D. H. M. (1972). Radio-tracking of warthogs: some results and their bearing on studies of game tse-tse fly relationships. *In* "Proceedings

of a Symposium of Biotelemetry", pp. 109–129. (CSIR Symp. S 57), Pretoria.

Cumming, D. H. M. (1975a). A technique for the capture of warthog. *E. Afr. Wildl. J.* **13**.

Cumming, D. H. M. (1975b). A field study of the ecology and behaviour of warthog. *Mus. Mem.* **7**, Salisbury.

Curry-Lindhal, K. (1961). "Contribution à l'étude des vertébrés terrestres en Afrique tropicale." Inst. Parcs Natn. Congo et Ruanda. Brussels.

Dagg, A. I. (1960a). Food preferences of the giraffe. *Proc. Zool. Soc. London* **135**, 640–642.

Dagg, A. I. (1960b). Gaits of the giraffe and the okapi. *J. Mammal.* **41**, 282.

Dagg, A. I. (1962a). The role of the neck in the movements of the giraffe. *J. Mammal.* **43**, 88–97.

Dagg, A. I. (1962b). The subspeciation of the giraffe. *J. Mammal.* **43**, 550–552.

Dagg, A. I. (1962c). The distribution of the giraffe in Africa. *Mammalia* **26**, 497–505.

Dagg, A. I. (1962d). Giraffe movements of the neck. *Nat. Hist.* **71**, 7, 44–51.

Dagg, A. I. (1965). Sexual differences in giraffe skulls. *Mammalia* **29**, 610–612.

Dagg, A. I. (1968). External features of giraffe. *Mammalia* **32**, 657–669.

Dagg, A. I. (1970). Tactile encounters in a herd of captive giraffe. *J. Mammal.* **51**, 279–87.

Dagg, A. I. (1971). *Giraffa camelopardalis. Mammal. Species* **5**, 1–8.

Dagg, A. I. (1974). Locomotion of the camel, *Camelus dromedarius. J. Zool. London* **174**, 67–78.

Dagg, A. I. and Taub, A. (1970). Flehmen. *Mammalia* **34** (4), 686–695.

Darling, F. F. (1950). Social life in ungulates. *Colloques internes du CNRS, Paris* **34**, 222.

Darling, F. F. (1960). "Wildlife in an African Territory." Oxford University Press.

Dasmann, R. F. and Mossman, A. S. (1962). Abundance and population structure of wild ungulates in some areas of Southern Rhodesia. *J. Wildl. Mgmt* **26** (1), 101–104.

Dasmann, R. F. and Mossman, A. S. (1962). Reproduction in some ungulates in Southern Rhodesia. *J. Mammal.* **43** (4), 533–537.

Davis, J. A. (1965). A preliminary report on the reproductive behaviour of the small Malayan chevrotain, *Tragulus javanicus* in New York Zoo. *Int. Zoo Yearbook* **5**, 42–44.

Davis, M. (1949). Parturition in the Nubian giraffe, *Giraffa camelopardalis Mammalia* **30**, 306–307.

Deane, N. N. (1962). Bushpig and warthog feeding. *Lammergeyer* **2** (1).

Dekeyser, P. (1955). Les mammifères de l'Afrique noire française. Paris.

Dekeyser, P. (1960). Encore des Céphalophes carnassiers. *Notes africaines* **88**, 29–130.

Denis, A. (1961). The hippos of Lake Baringo. *Oryx* **7**.

Deraniyagala, P. (1945). Some fossil animals from Ceylon. *J. Ceylon Asiatic Soc.* **36**, 80.

D'Huart, J. P. (1971). Révision et nouvelles recherches sur la biologie du

Phacochère, *Phacochoerus aethiopicus* Pallas. Mémoire de Licence. Univ. Catholique Louvain, non publiée. (In Monfort, 1974).
Dietrich, W. O. (1928). Pleistozäne deutchostafrikanische Hippopotamus-Reste. *Wiss. Ergebn. Oldoway Exped.* 3, 3–41.
Dinesen, I. (1937). "Out of Africa." Random House, New York.
Dodds, D. G. and Patton, D. R. (1968). Report to the Government of Zambia on the wildlife and land use survey to the Luangwa Valley. U.N. Devlop. Programme FAO 2591, Rome.
Dönhoff, G. C. (1942). Zur Kenntniss des afrikanischen Waldschweines (*Hylochoerus meinertzhageni*). *Zool. Gart.* (*NF*) **14**, 192–200.
Dönhoff, G. C. (1972). *In* "Animal Life Encyclopaedia" (Grzimek, B. ed.), Van Nostrand and Reinhold, New York.
Doorn, C. van (1967). Einiges über Giraffen and ihre Zucht und Haltung in Rotterdamer Zoo. *Freunde Köln Zoo* **10**, 79.
Doorn, C. van (1972). *In* "Animal Life Encylopaedia" (Grzimek, B. ed.), Van Nostrand and Reinhold, New York.
Dorst, J. and Dandelot, P. (1970). "A Field Guide to the Larger Mammals of Africa." Collins, London.
Dubost, G. (1963). Un ruminant à régime alimentaire partiellement carné: le chevrotain aquatique. *C.R. Acad. Sci. Paris* **256**, 1359–1360.
Dubost, G. (1964a). Précisions ostéologiques et dentaires et découverte d'os du mufle chez le chevrotain aquatique. *Biologia Gabonica* **1** (1), 25–29.
Dubost, G. (1964b). Un ruminant à régime alimentaire partiellement carné: le chevrotain aquatique. *Biologia Gabonica* **1**, 21–23.
Dubost, G. (1965a). Quelques traits remarquables du comportement de *Hyemoschus aquaticus*. *Biologia Gabonica* **1** (3), 283–287 & 313–318.
Dubost, G. (1965b). Glande préputiale du chevrotain aquatique, *Hyemoschus aquaticus* Ogilby. *Extrait Biologia Gabonica* **1** (4), 313–318.
Dubost, G. (1968). Les niches écologiques des forêts tropicales Sud-americaines et africaines. Sources de convergences remarquables entre rongeurs et artiodactyles. *Extrait Terre et Vie* **1**, 1968, 3–28.
Dubost, G. (1975). Le comportement du chevrotain africain *Hyemoschus aquaticus*. *Z. Tierpsychol.* **37**, 403–501.
Dubost, G. (1978). Un aperçu sur l'écologie du chevrotain africain, *Hyemoschus aquaticus* Ogilby, Artiodactyle Tragulidé. *Mammalia* **42** (1), 1–62.
Dubost, G. and Terrade, R. (1970). La transformation de la peau des Tragulidae en bouclier protecteur. *Mammalia* **34** (3), 505–512.
Duncan, W. R. H. and Garton, G. A. (1968). The fatty acid composition and intramolecular structure of triglycerides from adipose tissue of the hippopotamus and the African elephant. *Comp. Biochem. Physiol.* **25**, 319–325.
Dutt, R. H., Simpson, E. C., Christian, J. C. and Barnhart, C. E. (1959). Identification of preputial glands as the site of production of sexual odour in the boar. *J. An. Sci.* **18**, 1557.
Eddy, T. A. (1961). Foods and feeding patterns of the collared peccary in South Arizona. *J. Wildl. Mgmt* **25** (3), 248–257.
Edmond-Blanc, F. (1960). Contribution à l'étude du comportement et de la composition de la nourriture du bongo (*Boocerus eurycerus isaaci*) et de

l'hylochère (*Hylochoerus meinertzhageni*) du versant sud du Mont Kenya. *Mammalia* **24** (4), 538–541.

Eisenberg, J. F. and Lockhart, M. (1972). An ecological reconnaissance of Wilpattu National Park Ceylon. *Smiths. Contrib. Zool.* **101**.

Eisenberg, J. F. and McKay, G. M. (1974). Comparisons of ungulate adaptations in the new world and the old world tropical forests with special reference to Ceylon and the rainforests of central America. *In* "The Behaviour of Ungulates and its Relation to Management." (Geist, V. and Walther, F. eds), IUCN Publ. 24.

Evans, J. T. R. (1949). Rinderpest and tripanosomiasis. *Sudan Wild Life* **1** (1), 7–9.

Ewer, R. F. (1956). Fossil Suids of the Transvaal caves. *Proc. Zool. Soc. London* **127**, 527–544.

Ewer, R. F. (1958a). A collection of *Phacòchoerus aethiopicus* teeth from the Kalkbank Middle Stone Age site, Central Transvaal. *Palaeont. Afr.* **5**, 5–20.

Ewer, R. F. (1958b). Adaptive features in the skulls of African Suids. *Proc. Zool. Soc. London* **131**, 135–155.

Ewer, R. F. (1958c). The fossil Suidae of Makapansgat. *Proc. Zool. Soc. London* **130**, 329–372.

Ewer, R. F. (1968). "Ethology of Mammals." Logos Press, London.

Ewer, R. F. (1970). The head of the forest hog, *Hylochoerus meinertzhageni*. *E. Afr. Wildl. J.* **8**, 43–52.

Fairall, N. (1968). The reproductive seasons of some mammals in the Kruger National Park. *Zool. Afr.* **3**, 189.

Field, C. R. (1968a). A comparative study of some wild ungulates in the Queen Elizabeth National Park Uganda. Prelim. Report. *In* "Comparative Nutrition of Wild Animals." Symp. Zool. Soc. Lond. No. 21. (Crawford, M. A. ed.), pp. 135–151. Academic Press. London and New York.

Field, C. R. (1968b). Food habits of some wild ungulates in Uganda by analysis of stomach contents. *E. Afr. Wildl. J.* **10**.

Field, C. R. (1970a). Preliminary report of the food habits and nutrition of the giraffe in the Kidepo Valley National Park. (Report unpubl.)

Field, C. R. (1970b). A study of the feeding habits of *Hippopotamus amphibius* Linn. in the Queen Elizabeth National Park Uganda with some management implications. *Zool. Afr.* **5**, 71–86.

Field, C. R. (1970c). Observations on the food habits of tame warthog and antelope in Uganda. *E. Afr. Wildl. J.* **8**, 1–18.

Field, C. R. and Blankenship, L. H. (1973). Nutrition and reproduction of Grant's and Thomson's gazelles, Coke's Hartebeest and giraffe in Kenya. *J. Reprod. Fert.* **19**, 287–301.

Field, C. R. and Laws, R. M. (1970). The distribution of the larger herbivores in the Queen Elizabeth National Park Uganda. *J. Appl. Ecol.* **7**, 273–294.

Field, C. R. and Ross, I. C. (1976). The savanna ecology of the Kidepo Valley National Park I: Feeding ecology of elephant and giraffe. *E. Afr. Wildl. J.* **14** (1).

Finlayson, R. (1964). Vascular disease in captive animals. *In* "Cardiovascular Anatomy and Pathology" Symp. Zool. Soc. London No. 11. (Harrison, R. G. and Hill, K. R. eds). Academic Press, London and New York.

Flerow, C. (1931). On the generic characters of the family Tragulidae. *C.R. Acad. Sci. USSR*, **1931**.

Forsyth, J. (1897). On the species of *Potamochoerus*, the bushpigs of the Ethiopian region. *Proc. Zool. Soc. London* 359–370.

Foster, G. B. (1966). The giraffe of Nairobi National Park; home range, sex ratios, the herd and food. *E. Afr. Wildl. J.* **4**, 139–148.

Foster, G. and Coe, M. (1968). The biomass of game animals in Nairobi National Park. 1960–66. *J. Zool. London* **155** (4), 413–425.

Foster, G. B. and Dagg, A. I. (1972). Notes on the biology of the giraffe. *E. Afr. Wildl. J.* **10** (1), 1–6.

Foster, G. and Kearney, D. (1967). Nairobi National Park Game census 1966. *E. Afr. Wildl. J.* **5**, 112–120.

Foster, G. and McLaughlin, R. (1968). Nairobi National Park Game census 1967. *E. Afr. Wildl. J.* **6**, 152–154.

Frädrich, H. (1965). Zur Biologie und Ethologie des Warzenschweines (*Phacochoerus aethiopicus* Pallas.) unter Berücksichtigung des Verhaltens anderer Suiden. *Z. Tierpsychol.* **22** (3, 4), 328–393.

Frädrich, H. (1966). Breeding and handrearing warthogs, *Phacochoerus aethiopicus* in Frankfurt Zoo. *Int. Zoo Yearbook* **6**, 200.

Frädrich, H. (1967). Das Verhalten der Schweine und Hippo. *In* "Handbuch der Zoologie" pp. 1–44. De Gruyter, Berlin.

Frädrich, H. (1972). *In* Grzimek 1972.

Frädrich, H. (1974). A comparison of behaviour in Suidae. *In* "The Behaviour of Ungulates and its Relation to Management" (Geist, V. and Walther, F. eds), IUCN Publ. 24.

Fraipont, J. (1907). Okapia. Contribution à la faune du Congo. *Ann. Mus. Congo, Brussels.* **1**.

Fraipont, J. (1908). L'Okapi ses affinités avec les giraffidés vivants et fossiles. *Bull. Acad. Roy. Belg. Sci.* **12**.

Fraser, A. F. (1968). "Reproductive Behaviour in Ungulates." Academic Press, London and New York.

Fraser, F. C. (1951). Vestigial metapodials in the okapi and the giraffe. *Proc. Zool. Soc. London* **121**, 315–317.

Frechkop, S. (1944). Exploration du Parc National du Kagera. S. Frechkop Bruxelles.

Frechkop, S. (1946). De l'Okapi et les affinités des giraffidés avec les antelopes. *Bull. Hist. Nat. Belg.* **22**, 1–28.

Frechkop, S. (1948a). Sur quelques caractères du crâne chez les Ongulés. *Bull. Mus. Roy. Hist. Nat. Belg.* **24** (15), 1–8.

Frechkop, S. (1948b). Du pélage du chevrotain aquatique. *Bull. Mus. Roy. Hist. Nat.* **24** (28). 1–8.

Frechkop, S. (1955a). Super-ordre des ongulés. *In* "Traité de Zoologie." Volume 17 Mammifères Systematique (Grassé P. P., ed.) pp. 484–1167. Masson et Cie, Paris.

Frechkop, S. (1955b). Ordre des Artiodactylés. *In* "Traité de Zoologie." Vol. 17. Mammifères Systematique (Grassé, P. P., ed.), pp. 501–693. Masson et Cie, Paris.

Frechkop, S. (1955c). Famille des Giraffidés. *In* "Traité de Zoologie." Vol. 17. Mammifères Systematique (Grassé, P. P., ed.), pp. 660–667. Masson et Cie, Paris.

Friant, M. (1952a). Recherches sur le developpement du cerveau de la Girafe. *Acta Anat.* **21** (3), Bâle.

Friant, M. (1952b). Les caractéristiques fondamentales du cerveau des Giraffidés. *C.R. Acad. Sci. Paris.*

Friant, M. (1954). Sur la morphologie du troisieme sillon arque du cerveau chez les ongulés artiodactylés. *Acta Anat.* **22**.

Funaioli, U. and Simonetta, A. (1966). The mammalian fauna of the Somali Republic: status and conservation problems. *Monit. Zool. Ital.* **74**.

Gaudry, A. (1876). Sur un hippopotame fossile découvert à Bône (Algerie). *Bull. Soc. Geol. Fr.* **3** (4), 501–504.

Gauthier-Pilters, H. (1954). Untersuchungen über angeborene Verhaltenweisen bei Tylopoden. *Z. Tierpsychol.* **11**, 213–303.

Gauthier-Pilters, H. (1955). Observations éthologiques sur les Tylopodes. *Mammalia* **19**, 399–415.

Gauthier-Pilters, H. (1959). Angriffs and Kampfsverhalten des Dromedar, Geburt und Verhaltensentwicklung des Jungtieres in der N. W. Sahara. *Z. Tierpsychol.* **16** (5).

Gauthier-Pilters, H. (1961). Observations sur l'écologie du dromedaire dans le Sahara. *Mammalia* **25**, 195–280.

Gauthier-Pilters, H. (1974). The behaviour and ecology of camels in the Sahara, with special reference to nomadism and water management. *In* "The Behaviour of Ungulates and its Relation to Management." (Geist, V. and Walther, F. eds), IUCN Publ. 24.

Geigy, R. (1955). Observations sur les phacochères du Tanganyika. *Rev. Suisse Zool.* **62**, 139–163.

Geist, V. (1966). The evolution of horn-like organs. *Behaviour* **28**, 176–214.

Geist, V. (1968). Horn-like structures as rank symbols guards and weapons. *Nature, London* **220**, 813.

Gentry, A. W. and Gentry, A. (1970). Fossil Camels in Kenya and Tanzania. *Nature, London* **222**, 5196, 898.

Gijzen, A. (1959). "Das Okapi." Neue Brehm Bücherei.

Giraud, H. (1948). Contribution à l'étude du *Phacochoerus aethiopicus*. *Mammalia* **12**, 54–66.

Glatzel, H. (1962). Über die Morphologie und Histologie des Giraffenauges. *S. B. Ges. Naturf. Fr.* **2**, 150–168.

Glover, P. E. (1968). The role of fire and other influences on the savanna habitats with suggestions for further research. *E. Afr. Wildl. J.* **6**, 131–137.

Godina, A. J. (1964a). On the evolutionary trends in the Giraffe family. *Dok. Sov. Paleont. Prob.* **8**, 51–57.

Godina, A. J. (1964b). On certain problems of evolution in the Giraffidae (in Russian) *Byull. Mosk. Obshch. Ispyt, Prir. Geol.* **30** (5), 146–147.

Goetz, R. and Budzt-Olsen, O. (1955). The circulation of the giraffe. Scientific Safari. *S. A. Med. J., Cape Town* **29**, 773–778.
Goodwin, J. (1939). First white giraffe seen in Kenya. *Ill. Lond. News* **194**.
Goodwin, J. (1956). Nature's Skyscrapers. *Anim. Kingdom* **59**, 66–73.
Gowers, W. (1951). Some waterside reactions. *Zoo Life London* **6**, 63–65.
Gratiolet, P. (1967). Recherches sur l'anatomie de l'hippopotame. *Thèse Paris*, 1–405.
Graupner, H. (1928). Die Giraffe in Geschichte und Kunst. *Zool. Gart. (NF)* **1**.
Green, D. A. and Jewell, P. A. (1965). A method of measuring food passage rate in pigs by means of polystyrene markers. *Brit. Vet. J.* **121**, 83–89.
Grzimek, B. (1956a). Einige Beobachtungen an Wildtieren in Zentral Afrika. *Z. Tierpsychol.* **13**, 143–150.
Grzimek, B. (1956b). Schlaf von Giraffen und Okapi. *Naturwiss.* **43**, 406.
Grzimek, B. (1970). "Among Animals of Africa." Collins, London.
Grzimek, B. (1972). "Animal Life Encyclopaedia." Van Nostrand and Reinhold, New York.
Grzimek, M. and Grzimek, B. (1960). Census of plain animals in Serengeti. *J. Wildl. Mgmt* **24** (1).
Guggisberg, C. A. W. (1961). "Simba the Life of the Lion." Howard Timmings, Cape Town.
Guggisberg, C. A. W. (1969). "Giraffes." Golden Press New York; Arthur Baker, London.
Guiraud, M. (1948). Contribution à l'étude du *Phacochoerus aethiopicus* Pallas. *Mammalia* **12** (3), 55–66.
Gundlach, H. (1967). Tagesperiodik und Verhalten beim Wildschwein, *Sus scrofa*. *Nachr. Akad. Wissenschaft. Göttingen* **10**, 120.
Gundlach, H. (1968). Brutfürsorge, Brutpflege, Verhaltensontogenese und Tagesperiodik bein Europaischen Wildschein, *Sus scrofa* L. *Z. Tierpsychol.* **25**, 955–995.
Gutzwiller, R. (1956). Plantes fouragères de l'Okapi, *Okapia johnstoni* Sclater. *Acta Trop. Basel* **13**, 259–261.
Hafez, E. S. E. and Signoret, J. P. (1969). The behaviour of swine. *In* "The Behaviour of Domestic Animals." 2nd ed. (Hafez, Simplion and Jackaway, eds), Balliere Tindall and Cox, London.
Hall-Martin, A. J. (1974a). A note on the seasonal utilisation of different vegetation types by giraffe. *S. Afr. J. Sci.* **70**, 122–123.
Hall-Martin, A. J. (1974b). Food selection by Transvaal lowveld giraffe as determined by analysis of stomach contents. *J. S. Afr. Wildl. Mgmt Ass.* **4** (3), 192–202.
Hall-Martin, A. J. and Basson, W. D. (1974). Seasonal chemical composition of the diet of the Transvaal lowveld giraffe. *S. Afr. J. Wildl. Mgmt. Ass.* **4**.
Hall-Martin, A. J., Skinner, J. D. and Van Dyk, J. M. (1975). Reproduction in the giraffe in relation to some environmental factors. *E. Afr. Wildl. J.* **13**.
Haltenorth, Th. (1963). Klassification der Säugetiere; Artiodactyla 1 (18), 1–167. *In* Kukenthal's Handbuch der Zoologie, **8**, 32.
Harrison, H. (1936). The Shinyanga Game Experiment; a few of the early observations. *J. An Ecol.* **5**, 271–293.

Harrison, R. J. and Tomlinson, J. D. (1964). Observations on diving seals and certain other mammals. *In* "The Biology of Survival." Symp. Zool. Soc. London, No. 13, (Edholm, O. G. ed.), pp. 59–69. Academic Press, London and New York.

Hediger, H. (1950). "Wild Animals in Captivity." Butterworth, London.

Hediger, H. (1951). Observations sur la psycologie animale dans les parcs nationaux du Congo Belge. 1, Mission Hediger-Verschuren. Inst. Parcs Natn Congo Belge, Brussels.

Henry, V. G. (1968). Length of oestrus cycle and gestation in European wild hogs. *J. Wildl. Mgmt* **32** (2), 406–408.

Henshaw, J. (1972). Notes and Records. *E. Afr. Wildl. J.* **10**, 151.

Hermann, C. L. (1959). La Giraffa. *Giardino Zoologico* **4**, 3–6.

Herre, W. (1936). Untersuchungen an Hirnen von Wild und Hausschweinen. *Verh. Detsch. Zool. Ges.*

Herre, W. (1952). Studien über die wilden und domestizierten Tylopoden südamerikas. *Zool. Gart.* **19**.

Hershkovitz, P. (1968). Metachromism or the principle of evolutionary change in mammalian tegumentary colours. *Evolution* **22**.

Heuschele, W. P. and Coggins, L. (1965). Isolation of African swine fever virus from a giant forest hog. *Bull. Epiz. Dis. Afr.* **13**, 255–256.

Hildebrand, M. (1966). Analysis of symmetrical gaits in tetrapods. *Folia Biotheoretica* **6**, 9–22.

Hillaby, J. (1968). Wild Porker. *New Scientist* **39** (614), 542.

Hirst, S. M. (1965). Timbavati Private Nature Reserve. *Afr. Wildlife* **19** (3), 228–235.

Hirst, S. M. (1966). Immobilization in the Transvaal giraffe, *Giraffa camelopardalis giraffa*, using an oripavin derivative. *J. S. Afr. Vet. Med. Ass.* **37**, 85.

Hirst, S. M. (1969a). Road-strip census techniques for wild ungulates in African woodland. *J. Wildl. Mgmt Ass.* **24**, 1–15.

Hirst, S. M. (1969b). Predation as a regulating factor of wild ungulates populations in a Transvaal lowveld Nature Reserve. *Zool. Afr.* **4**, 199–230.

Hofmann, R. R. (1968). Comparisons of the rumen and omasum structure in East African game ruminants in relation to their feeding habits. *In* "Comparative Nutrition of Wild Animals." Symp. Zool. Soc. London, No. 21, (Crawford, M. A. ed.), pp. 179–194. Academic Press, London and New York.

Hofmann, R. R. (1973). The Ruminant Stomach. *East African Monographs in Biology* **2**, 113–124.

Hofmann, R. R. and Stewart, D. R. M. (1972). Grazer or Browser: a classification based on the stomach structure and feeding habits of East African ruminants. *Mammalia* **36**, 226–240.

Hofmeyer, J. M. (1970). A review of the food preferences and feeding habits of some indigenous herbivores in the Ethiopian faunal region and some studies on animal-plant relationships. *Proc. S. Afr. Soc. An. Prod.* **9**, 89–99.

Hoier, R. (1950). Les hippopotames au Parc National Albert. *Zooleo* **5**, 15–21.

Hoier, R. (1955). L'Hippopotame. *In* "Le grand livre de la fauna africaine et de la chasse" Vol. 1. (Edmond-Blanc ed.), pp. 41–51. Schmidt, Zurich.
Hooijer, D. A. (1950). The fossil hippopotamidae of Asia with notes on the recent species. *Zool. Verhandl. Leiden* **8**, 1–124.
Hooijer, D. A. (1962). Miocene mammalia of the Congo. *Ann. Mus. Afrique Tervuren* **46**.
Hoppe, P., Kay, R. N. B. and Maloiy, G. M. O. (1974). Salivary secretion in the camel. *J. Physiol.* **244** (1), 32–33.
Hopwood, A. T. and Hollyfield, J. P. (1954). An annotated bibliography of the fossil mammals of Africa (1742–1950). "Fossil Mammals of Africa" Vol. 8, pp. 1–194. British Museum (Nat. Hist.) London.
Howell, F. C. (1968). Omo research expedition. *Nature, London* **219**, 576–672.
Howell, F. C., Fichter, R. and Wolff, R. (1969). Fossil camels in the Omo beds, Southern Ethiopia. *Nature, London* **223**, 15–152.
Hughes, I. (1970). A report on the movement/occupation patterns of migratory game in the Samburu/Isiolo Game Reserve and adjacent Hunting Blocks (Unpublished).
Hungate, R. E. (1966). "The Rumen and its Microbes." Academic Press, London and New York.
I.B.A.H. (1962). The geographical distribution of the warthog and domestic pigs in Africa. *Bull. Epiz. Dis. Afr.* **10**, 91–94.
Immelmann, K. and Gebbin, H. (1962). Schlaf bei Giraffiden. *Z. Tierpsychol.* **19**, 84–92.
Ingram, D. L. (1965). Evaporative cooling in the pig. *Nature, London* **207**, 415–416.
Innis, A. C. (1958). The behaviour of the giraffe (*Giraffa camelopardis*) in eastern Transvaal. *Proc. Zool. Soc. London* **131** (2), 245–278.
Innis, A. C. (1968). The inheritance of external features of giraffe. *Mammalia* **32**.
Ionides, C. J. P. (1955). Nature notes. *Afr. Wildlife* **9** (1).
Ionides, C. J. P. (1965). "A Hunter's Story." W. H. Allen, London.
Irving, L. (1956). Physiological insulation of swine as bare-skinned animals. *J. Appl. Physiol.* **9**, 414–420.
Jamdar, M. N. (1961). Comparative anatomy of the bony system of the camel (axial skeleton, 53–54. Bones of the skull 325–328. *Indian Vet. J.* **38**.
Jarvis, C. (ed.) (1968). Gestation period of an okapi at Bristol Zoo. *Int. Zoo Yearbook* **8**.
Jarvis, C. and Morris, D. (eds.) (1960a). Breeding notes on the hippopotamus and giraffe at Cleveland Zoo. *Int. Zoo Yearbook* **2**.
Jarvis, C. and Morris, D. (1960b). Breeding notes on the reticulated giraffe at Cheyenne Mountain Zoo. *Int. Zoo Yearbook.* **2**.
Jensen, A. (1934). The sacred animal of the god Set. *Kgl. Danske Vidensk. Selsk. Biol. Med. Copenhagen.*
Jobaert, A. J. (1958). Le Potamochère. *Zooleo* **44**, 145–154.
Joleaud, L. (1933). Etudes de géographie zoologique sur le Bérberie. Les Pachydermes. Les sangliers et les phacochères. *Rev. Géogr. Maroc.* **17**, 177–192.
Jones, F. (1949). Evolution of the giraffe. *Nature, London* **164**.

Jones, O. G. (1954). Endeavour to rear a baby giraffe. *Vet. Rec.* **66**, 417.
Kanan, C. V. (1960). Notes on the vertebral column ribs and sternum of the camel. *Sudan J. Vet. Sci.* **1**, 84–91.
Kattinger, E. (1942–49). Bemerkungen über Tigerpferde. *Z. Säugetierk.* **17**, 115–122.
Kellas, L. M., Lennep, E. W. van and Amoroso, E. C. (1958). Ovaries of some foetal and prepubertal giraffes. *Nature, London* **181**, 487–488.
Kerbert, C. (1922). Over Dracht, geborte, puberteit en levensduur van *Hippopotamus amphibius* Linn. *Bijdr. Dierk.* **22**, 185–191.
Kirchshofer, E. (1970). Notiz über ein Steibgeburt beim Flusspferd, *H. amphibius* Linn. Einigen Bemerkungen zur Vehreprungsrate des Frankfurter Flusspferden. *Säugetierk.* 33 (1), 27–34.
Koch, W. (1935). Rudimentäre Metapodien beim Okapi. *Z. Säugetierk.* **10**, 148–150.
Koopman, K. F. (1967). Artiodactyls. *In* (Anderson, S. and Knox, J. eds.), "Recent Mammals of the World." New York.
Krumbiegel, I. (1939). Die Giraffe. Monograph. *Wildsäugetiere* **8**, 98 pp.
Krumbiegel, I. (1966). Gabelungspuren an Giraffenhornen. *Säugetierk Mitt.* **14**, 107–108.
Kruska, D. (1970). On the evolution of the artiodactylan brain with species reference to the Suina Gray 1868. *Z.f. Säugetierk.* **35** (4), 214–238.
Kruuk, H. (1972). "The Spotted Hyaena." University of Chicago Press, U.S.A.
Kurt, F. (1963). Zur Carnivorie bei *Cephalophus dorsalis*. *Z.f. Säugetierk* **28**.
Lamprey, H. F. (1963). Ecological separation of large mammal species in the Tarangire Game Reserve, Tanganyika. *E. Afr. Wildl. J.* **1**, 63–93.
Lamprey, H. F. (1964). Estimation of the large mammals densities, biomass and energy change in the Tarangire Game Reserve and Masai steppe of Tanganyika. *E. Afr. Wildl. J.* **2**, 1–46.
Lamprey, H. F. (1967). Notes on the dispersal and germination of some tree seeds through the agency of mammals and birds. *E. Afr. Wildl. J.* **5**, 179.
Landscheere, J. de (1957). Observations concernant l'Okapi. *Zoo Antwerp*, **23**, 12–25.
Lang, E. M. (1956). Haltung und Brunst von Okapia in Epulu. *Säugetierk. Mitt.* **4**, 49–52.
Lang, E. M. (1957). Stimmlicher Kontakt von Okapis untereinander. *Säugetierk. Mitt.* **5**, 171.
Langer, P. (1974). Stomach evolution in the artiodactyla. *Mammalia* **38** (2).
Langman, V. A. (1973a). Radio-tracking giraffe for ecological studies. *J. S. Afr. Wildl. Mgmt Ass.* 3 (2), 75–78.
Langman, V. A. (1973b). The immobilization and capture of giraffe. *S. Afr. J. Sci.* **69**. 200–203.
Lankester, E. R. (1903). Hair-worls in the Okapi. *Proc. Zool. Soc. London* **2**, 337–340.
Lankester, E. R. (1907a). The origin of the lateral horns of the giraffe in foetal life on the area of the parietal bones. *Proc. Zool. Soc. London* **1**, 100–115.
Lankester, E. R. (1907b). On the existence of rudimentary antlers in the okapi. *Proc. Zool. Soc. London* **1**, 126–135.

Lankester, E. R. (1907c). Parallel hair fringes and colour striping on the face of foetal and adult giraffe. *Proc. Zool. Soc. London* **1907**.
Lankester, E. R. (1910). "Monograph of the Okapi" (with the assistance of W. G. Ridewood). Alard and Son, London.
Laufer, B. (1928). The giraffe in history and art. *Field Mus. Nat. Hist. Chicago* **27**.
Lavocat, R. (1955). Ruminants fossiles. *Traité de Zoologie* **17**, 668–693.
Lavocat, R. (1958). Classification des Ongulés d'après leur origine et leur évolution. *Mammalia* **22**, 28–40.
Lavocat, R. (1961). Etude systématique de la faune des mammifères et conclusions générales. *Serv. Géol. Maroc* **155**.
Lawrence, W. E. and Rewell, R. E. (1948). Cerebral blood supply of Giraffidae. *Proc. Zool. Soc. London* **118** (1), 202–212.
Laws, R. M. (1965). Observations on reproduction in the hippopotamus. *J. Reprod. Fert.* **9**, 369–370.
Laws, R. M. (1967). Interactions between elephant and hippopotamus populations and their environments. Paper presented at East African Wildlife-Land Use Symposium.
Laws, R. M. (1968). Dentition and ageing of the hippopotamus. *E. Afr. Wildl. J.* **6**, 19–52.
Laws, R. M. and Clough, G. (1965). Observations on reproduction in the hippopotamus *Hippopotamus amphibius*. *J. Reprod. Fert.* **9**, 369–370.
Laws, R. M. and Clough, G. (1966). Observations on reproduction in the hippopotamus Hippopotamus amphibius. *In* "Comparative Biology of Reproduction in Mammals" Symp. Zool. Soc. London No. 15. (Rowlands, I. W. ed.), p. 117–140. Academic Press, London and New York.
Laws, R. M. and Parker, I. S. C. (1968). Elephant populations in East Africa. *In* "Comparative Nutrition of Wild Animals" Symp. Zool. Soc. London No. 21. (Crawford, M. A. ed.), p. 345. Academic Press, London and New York.
Laws, R. M., Parker, I. C. S. and Johnstone, R. C. B. (1975). "Elephants and their Habitats." Clarendon Press, Oxford.
Leakey, L. S. B. (1943). New fossil Suidae from Shungura Omo. *J. E. Afr. Uganda Nat. Hist. Soc.* **17**, 45–61.
Leakey, L. S. B. (1958). Some East African Pleistocene Suidae. "Fossil Mammals of Africa" Vol. 14, p. 133. British Museum (Nat. Hist.) London.
Leakey, L. S. B. (1965). "Olduvai Gorge 1951–1961. Vol. 1, "Fauna and Background." pp. 1–109. Cambridge University Press.
Ledger, H. P. (1968). Body composition as a basis for a comparative study of some East African animals. *In* "Comparative Nutrition of Wild Animals" (Crawford, M. A. ed.) Symp. Zool. Soc. London No. 21, Academic Press, London and New York.
Lee, M. and Talbot, M. (1962). How much does it weigh? *Wildlife Nairobi* 3.
Leese, A. S. (1927). "A Treatise on the One-humped Camel." Haynes and Son, Stamford.
Leister, C. W. (1939). The wild pigs of the world. *Bull. New York Zool. Soc.* **42**, 130–139.

Leonardi, P. (1952). I suidi di Sahabi nella Sirtica (Africa settentrionale). *C.R. Acad. Nazion. deo XL ser. IV*, 4, 75–88.

Lesbre, F. X. (1903). Recherches anatomiques sur les Camelidès. *Arch. Mus. Hist. Nat. Lyons* **8**, 90–99.

Leuckart, F. S. (1843). Der Magen eines *Moschus javanicus*. *Arch. Anat. Physiol. u. Wiss. Med.* **1843**, 24–27.

Leuthold, W. (1977). Changes in tree population of Tsavo East National Park Kenya. *E. Afr. Wildl. J.* **15**, 61–69.

Leuthold, W. (1978). Ecology of the giraffe in Tsavo East National Park Kenya East Africa. *E. Afr. Wildl. J.* **16** (1), 1–20.

Leuthold, B. M. and Leuthold, W. (1972). Food habits of giraffe in Tsavo National Park Kenya. *E. Afr. Wildl. J.* **10**, 129–142.

Leuthold, B. M. and Leuthold, W. (1975). Temporal patterns of reproduction in ungulates of Tsavo East National Park Kenya. *E. Afr. Wildl. J.* **13** (3, 4).

Lock, J. M. (1967). Vegetation in relation to grazing and soils in Queen Elizabeth National Park Uganda. PhD. Thesis University of Cambridge.

Lock, J. M. (1972). The effects of hippo grazing on grasslands. *J. Ecology* **60**.

Longhurst, W. M. (1957). Results of a preliminary survey of the hippopotamus situation in Queen Elizabeth National Park Uganda. Game and Fisheries Department. Entebbe, Uganda.

Longhurst, W. M. (1966). Observations on apparent echo-ranging by hippo. *In* Proc. 3rd Ann. Conf. Biology, sonar and diving mammals. (Rice, C. E. ed.) Stanford Research Institute.

Lönnberg, E. (1905). Notes on the geographical distribution of the okapi. *Proc. Zool. Soc. London* **2**, 309–310.

Lönnberg, E. (1908). Remarks on some warthog skulls in the British Museum. *Proc. Zool. Soc. London* **1908**, 936–940.

Lönnberg, E. (1910). Contributions to the knowledge of the genus *Potamochoerus Arch. Zool.* **7**, 40.

Luck, C. P. (1967). The comparative morphology of the eyes of certain African Suiformes. *Vision Res.* **5**, 283–297.

Luck, C. P. and Wright, P. G. (1964). Aspects of the anatomy and physiology of the skin of the hippopotamus *(Hippopotamus amphibius)*. *Quart. J. Exp. Physiol.* **49**, 1–14.

Lydekker, R. (1904a). On the subspecies of *Giraffa camelopardalis*. *Proc. Zool. Soc. London* **1**, 202–227.

Lydekker, R. (1904b). On old pictures of giraffes and zebras. *Proc. Zool. Soc. London* **2**, 339.

Lydekker, R. (1908). Local variations in the giraffe. *Animal Life*, Sept.

Lydekker, R. (1910). Hornless okapis. *Ann. Mag. Nat. Hist.* **6**, 224–226.

Lydekker, R. (1914). The horns of the okapi. *Nature, London* **93**, 478–479.

Maberly, C. T. A. (1947). Giraffe noises. *Field, London* **189**.

Maberly, C. T. A. (1950). The African bushpig—sagacious and intelligent. *Afr. Wildlife* **4** (1), 14–18.

Maberly, C. T. A. (1963). "The Game Animals of Southern Africa." Nelson, Cape Town.

Maberly, C. T. A. (1966). African bushpigs. *Animals* **9** (9), 556–564.

Maberly, C. T. A. (1969). The bushpig is a family-man. *Natal Wildlife* **10** (1), 4–6.
MacFarlane, W. V. and Howard, B. (1970). "Water in the Physiological Ecology of Ruminants. Physiology of Digestion and Metabolism in the Ruminant." (Phillipson ed.), Oriel Press, Newcastle upon Tyne.
MacFarlane, W. V. and Siebert, B. D. (1967). Hydration and dehydration of desert camels. *Austr. J. Exp. Biol. Med. Sci.* **45**, 29.
MacFarlane, W. V., Morris, R. J. H. and Howard, B. (1962). Water metabolism of merino sheep and camels. *Austr. J. Sci.* **25**, 112.
MacFarlane, W. V., Morris, R. J. H. and Howard, B. (1963). Turnover and distribution of water in desert camels, sheep, cattle and kangaroos. *Nature, London* **197**, 270–271.
MacFarlane, W. V., Kinne, R., Walmsley, C. M., Siebert, B. D. and Peter, D. (1967). Vasopressins and the increase of water and electrolyte excretion by sheep, cattle and camels. *Nature, London* **214**, 979–981.
MacFarlane, W. V., Howard, B., Maloiy, G. M. O. and Hopcraft, D. (1972). Tritiated water in field studies of ruminant metabolism in Africa. *In* "Isotope Studies on the Physiology of Domestic Animals." I.A.E.A. SM 156/36.
Malbrant, R. and MacLatchy, A. (1949). Faune de l'équateur africain français II, Mammifères. *Encyclop. Biol.* **36**, 1–323.
Maloiy, G. M. O. (1971). Renal salt and water excretion in the one-humped camel. *Int. Congr. Physiol. Sci.* **25**, 365.
Maloiy, G. M. O. (Ed.) (1972a). Renal salt and water excretion in the camel (*Camelus dromedarius*). *In* "Comparative Physiology of Desert Animals" Symp. Zool. Soc. London No. 31. pp. 243–259. Academic Press, London and New York.
Maloiy, G. M. O. (Ed.) (1972b). Comparative physiology of desert animals. Symp. Zool. Soc. London No. 31. Academic Press, London and New York.
Maré, C. J. (1975). The role of wild pigs in the epidemiology of African swine fever. *In* "Wildlife Diseases." (Page, L. A. ed.) Plenum Press, New York.
Matthew, W. D. (1929). Critical observations upon Siwalik mammals. *Bull. Amer. Mus. Nat. Hist.* **56**, 437–560.
Matthews, L. H. (1969). "The Life of Mammals." Weidenfeld and Nicolson, London.
Maynard-Smith, J. and Savage, R. J. G. (1959). The mechanics of mammalian jaws. *S. Sci. Rev.* **40**, 289–301.
McBride, G. (1963). The "teat order" and communication in young pigs. *An. Behav.* **11**, 53–56.
Mejia, C. (1972a). Social behaviour and organisation of giraffe in the Serengeti National Park. Unpublished Report Serengeti Research Institute.
Mejia, C. (1972b). Two main aspects of social organisation of the Maisai giraffe: the social structure of males; the fight-necking complex and the mother/calf relationship (Unpublished).
Merle, R. (1952). L'hippopotame dans la nature. *La Nature Paris* **3209**, 271–273.

Miller, G. S. (1910). Description of a new species of hippo. *Smithsonian Misc. Coll.* **54**, 7.

Milne-Edwards, A. (1864). "Recherches anatomiques, zoologiques et paléontologiques sur la famille des chevrotains." Martinet, Paris.

Milstein, P. le S. (1971). The bushpig, *Potamochoerus porcus* as a problem animal in South Africa. *Proc. Entomol. Symp. Pretoria* 27 Sept., 1–29. (Mimeograph).

Mimram, R. (1962). "Les glandes occipitales du dromedaire." Cahiers de la Faculté des Sciences, Rabat.

Misonne, X. (1952). Quelques éléments nouveaux concernant *Hippopotamus imaguncula Hopwood. Bull, Inst. Roy. Sci. Nat. Belg.* **28**, 1–12.

Mohr, E. (1942). Das Riesen-Waldschwein, *Hylochoerus meinertzhageni. Zool. Gart.* **14** (4), 177–191.

Mohr, E. (1960). "Wilde Schweine. "Neüe Brehm Bücherei. Wittemberg Lutherstadt.

Moir, R. J. (1968). Ruminant digestion and evolution. *Handbook of Physiology* **5**, 2673–2694.

Monfort, A. (1972). Densités, biomasses et structures d'ongulés sauvages au Parc National de l'Akagera Rwanda. *Terre et Vie* **26**, 216–256.

Monfort, A. (1974). Quelques aspects de la biologie des phacochères, *Phacochoerus aethiopicus*, au Parc National de L'Akagera Rwanda. *Mammalia* **38** (2).

Monfort, A., Monfort, N. and Ruwet, J. C. (1973). Eco-éthologie des ongulés au Parc National de L'Akagera Rwanda. *Ann. Soc. Roy. Zool. Belg.* **103**, 177–208.

Montgomery, R. E. (1921). On a form of swine fever Occuring in British East Africa. *J. Comp. Path. Therap.* **34**, 159–191.

Moore-Berger, E. (1974). Utilization of the habitat by the reticulated giraffe in Northern Kenya. M.Sci. thesis, University of Nairobi.

Moreau, R. E. and Pakenham, R. H. W. (1941). The land vertebrates of Pemba, Zanzibar and Mafia: a zoogeographical study. *Proc. Zool. Soc. London* **110**.

Morris, D. and Jarvis, C. (Eds.). (1959). Pigmy hippopotamus bred at Washington Zoological Park. *Int. Zoo Yearbook* **1**, 45.

Moss, C. (1976). "Portraits in the Wild." Hamish Hamilton, London.

Moule, A. (1925). Some foreign birds and beasts in Chinese books. *J. R. As. Soc.* **1925**.

Mount, L. E. (1960). The influence of huddling and body size on the metabolic rate of the young pig. *J. Agric. Sci. Cambridge* **55**, 101–105.

Mount, L. E. (1968). "The Climatic Physiology of the Pig." Edward Arnold, London.

Muybridge, E. (1899). "Animals in Motion." London.

Naaktgeboren, C. (1969). Geburtkundliche Bemerkungen über die Hörner der neugeborene Giraffen. *Z. Säugetierk.* **34**, 375–379.

Nasimovic, A. A. (1966). *In* "Die Säugetiere der Sowietunion" (Heptner *et al.*, eds), G. Fisher Verlag, Jena.

Nesbit-Evans, E. M. (1970). The reaction of a group of Rothschilds giraffe to a new environment. *E. Afr. Wildl. J.* **8**, 53–62.

Neuville, H. and Derscheid, J. M. (1928–29). Recherches anatomiques sur l'okapi, *Okapia johnstoni* Scl. *Rev. Zool. Bot. Afr.* **16**.
Noack, T. (1891). Beiträge zur Kenntniss der Säugetierfauna von Ost and Zentralafrika. *Zool. Jhrb. Syst.* 2.
Noack, T. (1908). Die Giraffe des Sambesigebietes. *Zool. Anz.* 33.
Noirot-Timothée, C. (1968). Les cilies du rumen de *Hyemoschus aquaticus. Biol. Gabon.* **4**, 343–352.
Norton-Griffiths, M. (1975). The numbers and distribution of large mammals in Ruaha National Park Tanzania. *E. Afr. Wildl. J.* **13**, 2, 121.
Oats, L. G. (1972). Food preferences of giraffe in Transvaal lowveld woodland. *J. S. Afr. Wildl. Mgmt. Ass.* **2** (2), 21–23.
Olivier, R. (1974). Hippopotamus. Conservation bulletin 1. Wildlife Clubs of Kenya.
Olivier, R. and Laurie, W. A. (1974). Habitat utilization by hippopotamus in the Mara River. *E. Afr. Wildl. J.* **12**, 249–272.
Owen, R. (1841). Anatomy of warthog. *Proc. Zool. Soc. London* **1841**, 63–69.
Owen, R. (1868). "On the Anatomy of Vertebrates." Vol. 3, London.
Pearson, H. and Wright, A. I. (1968). Some observations on the rearing of an okapi calf, *Okapia johnstoni. Int. Zoo. Yearbook* **8**, 134–135.
Pellew, R. A. (1976). Giraffe ecology in the Serengeti. *In* Annual Report of the Serengeti Research Institute.
Peck, E. F. (1939). Salt intake in relation to cutaneous necrosis and arthritis of one humped camels in British Somaliland. *Vet. Rec.* **51**, 136–160.
Petrides, G. (1965). Advisory report on wildlife and national parks in Nigeria 1962. New York Spec. Publ. 18th Amer. Comm. Int. Wildlife Protection.
Petzsch, H. (1950). Zur Frage des Vorkommens ungefleckter albinotischer Giraffen. *Zool. Gart. (NF)* **17**.
Phillips, J. F. V. (1926). Wild pig (*Potamochoerus choiropotamus*) at Knysna: notes by a naturalist. *S. Afr. J. Sci.* **23**, 655–660.
Phillips, J. F. V. (1929). Some important vegetation communities in the central province of Tanganyika. *S. Afr. J. Sci.* **26**, 332–372.
Phillipson, A. T. (1970). "Physiology of Digestion and Metabolism in the Ruminant." Oriel Press, Newcastle upon Tyne, England.
Physick, R. (1972). Hippo behaviour. *Lammergeyer* **15**.
Pienaar, U. de V. (1963). The large mammals of the Kruger National Park, their distribution and present day status. *Koedoe* **6**, 1–37.
Pienaar, U. de V. (1967). The field immobilization and capture of *Hippopotamus amphibius* Linn. in their aquatic element. *Koedoe* **10**, 149–157.
Pienaar, U. de V. Van Wyck, P. and Fairall, N. (1966). An experimental cropping scheme of hippopotami in the Kruger National Park. *Koedoe* **9**, 1–34.
Pilgrim, G. (1925). The migration of Indian mammals. *Proc. 12th Ind. Sci. Congr. Sect. Geol.* 200–218.
Pilgrim, G. (1926). The fossil Suidae of India. *Palaeont, Indica* **8**, (4), 1–65, Calcutta.
Pilgrim, G. (1941). The dispersal of the Artiodactyla. *Biol. Rev.* **16**, 134–163.
Pitman, C. R. S. (1951). Annual Report of the Game Department. Govt. Printer, Entebbe, Uganda.

Plowright, W., Laws, R. M. and Rampton, C. S. (1964). Serological evidence for the susceptibility of the hippopotamus, *(H. amphibius)* Linn. to natural infection with rinderpest virus. *J. Hyg. Cambridge* **62**, 329–336.

Plowright, W., Parker, J. and Pierce, M. A. (1969). The epizootiology of African swine fever. *Vat. Rec.* **85** (12), 668–674.

Pocock, R. I. (1919). External characters of chevrotains. *Proc. Zool. Soc. London* **1919**, 1–11.

Pocock, R. I. (1936). Preliminary note on a new point in the structure of the feet of the okapi. *Proc. Zool. Soc. London* **1936**, 583–586.

Pocock, R. I. (1943a). The external characters of a forest hog *(Hylochoerus)* and of a *Babirussa* that died in the Society's gardens. *Proc. Zool. Soc. London* **113**, 36–42.

Pocock, R. I. (1943b). Some additional external characters of the okapi that died in the Society's gardens. *Proc. Zool. Soc. London* **113**, 31–35.

Pocock, R. I. (1946). The Okapi. *Zoo Life* **1**, 3–7.

Portman, A. (1952). "Animal Forms and Patterns." Faber and Faber, London.

Pournelle, G. H. (1955). Notes on the reproduction of a Baringo giraffe. *J. Mammal.* **36**.

Pournelle, G. H. (1957). Congo's okapi is here. *Zoonooz* **30**, 3–5.

Prozig, E. (Ed.). (1966). Das Verhalten landwirtschaftlicher Nutztiere. VEB Deutscher Landwirtschafttsverlag, Berlin.

Prickett, R. J. (1974). "The African Ark." Newton Abbot.

Prunier, D. (1946). Note sur les Suidés sauvages de Guinée. *Mammalia* **10**, 146–148.

Purohit, M. S. and Rathor, S. S. (1962). Stomach of the camel in comparison to that of the ox. *Ind. Vet. J.* **39**, 604–608.

Rahm, U. (1966). Les mammifères de la forêt équatoriale de l'est du Congo. *Ann. Mus. Roy. Afr. Centr. Sci. Zool.* **118**.

Rahm, U. and Christiaensen, A. (1963). Les mammifères de la région occidentale du lac Kivu. *Ann. Mus. Roy. Afr. Centr. Sci. Zool.* **118**.

Ralls, K. (1971). Mammalian scent marking. *Science* **171**, 443–449.

Rapp, W. (1843). Anatomische Untersuchungen uber das javanische *Moschus*-Tier. *Arch. Naturgeschich.* **9**, 43–54.

Rensch, B. (1954). Neuere Probleme der Abstammungslehre. Stuttgard.

Reucassel, D. (1971). Hippo to the rescue. *Afr. Wildlife* **25** (4).

Reventlow, A. (1949). The growth of giraffes and giraffe calves. *Bijdr. Dierkd.* **28**, 394–396.

Riet, van W. A. (1969). A study of hippo populations. *Afr. Wildlife* **23**, 263.

Robinson, E. (1949). "Evolution of the Giraffe." London.

Robinson, H. G. N., Gribble, W. D., Page, W. G. and Jones, G. W. (1965). Notes on the birth of a reticulated giraffe, *Giraffa camelopardalis antiquorum*. *Int. Zoo Yearbook* **5**, 49–52.

Rodhain, J. (1928–29). Les moeurs de l'okapi. *Rev. Zool. Bot. Afr.* **16**, 74–75.

Roth, H. H. (1965). Observations on the growth and ageing of warthog *(Phacochoerus aethiopicus)* Pallas 1766. *Z. Säugetierk.* **30**, 367–380.

Rothschild, M. and Neuville, H. (1906a). Sur *l'Hylochoerus meinertzhageni*. *C.R. Acad. Sci. Paris*, 646–648.

Rothschild, M. and Neuville, H. (1906b). *L'Hylochoerus meinertzhageni. Bull. Soc. Philomath. Paris* **9** (8), 141–164.

Rothschild, M. and Neuville, H. (1911). Recherches sur l'okapi et les girafes de l'est africain. *Ann. Sci. Nat. Zool.* **13**, 1–185.

Saint-Aubin, G. de (1961). Aperçu sur la forêt du Gabon. *Bois et Forêts des Tropiques* **78**, 3–17.

Sanderson, I. T. (1940). The mammals of the North Cameroon forest area. *Trans. Zool. Soc. London* **24**.

Sato, Shun (1978). Preliminary report of camelecology among the Rendille in Northern Kenya. Primate Research Institute, Kyoto University Japan.

Savoy, G. C. (1966). Breeding and hand-rearing of the giraffe (*Giraffa camelopardalis*) at Columbus Zoo. *Int. Zoo Yearbook* **6**, 202–204.

Schaffer, J. (1940). "Die Hautdrüsenorgane der Säugetiere. "Urban and Schwarzenberg, Berlin.

Schaller, G. (1972). "The Serengeti Lion: a study of predator-prey relations." University of Chicago Press, U.S.A.

Schaub, S. (1958). Simplicidentata. *In* "Traité de Paléontologie." Masson et Cie, Paris.

Schmidt, E. (1911). Untersuchungen über den Magen der Wiederkäuer, vornehmlich der Traguliden. Diss. Phil. Bern.

Schmidt-Nielsen, K. (1959). The physiology of the Camel. *Scient. Amer.* **201** (6), 140–151.

Schmidt-Nielsen, K. (1964). "Desert Animals Physiological Problems of Heat and Water." Oxford University Press, Oxford.

Schmidt-Nielsen, K., Schmidt-Nielsen, B., Houpt, T. R. and Jarnum, S. A. (1956a). The question of water storage in the stomach of the camel. *Mammalia* **20**, 1–11.

Schmidt-Nielsen, K., Schmidt-Nielsen, B., Houpt, T. R. and Jarnum, S. A. (1956b). Water balance of the camel. *Amer. J. Physiol.* **185**.

Schmidt-Nielsen, K., Schmidt-Nielsen, B., Houpt, T. R. and Jarnum, S. A. (1957a). Urea excretion in the camel. *Amer. J. Physiol.* **188**.

Schmidt-Nielsen, K., Schmidt-Nielsen, B., Houpt, T. R. and Jarnum, S. A. (1957b). Body temperature of the camel and its relation to water economy. *Amer. J. Physiol.* **188**, 103–112.

Schmidt-Nielsen, K., Crawford, E. C., Newsome, A. E., Rawson, K. S. and Hammel, H. T. (1967). Metabolic rate of camels; effect of body temperature and dehydration. *Amer. J. Physiol.* **212**, 341–346.

Schouteden, H. (1912–1913). Notes sur l'okapi. *Rev. Zool. Afr.* **2**, 482–485.

Schouteden, H. (1919–1920). Un okapi vivant en Belgique. *Rev. Zool. Afr.* **7**, 199–200.

Schouteden, H. (1928–1929). Un jeune okapi. *Rev. Zool. Bot. Afr.* **16**, 71–72.

Schouteden, H. (1950). Vue d'ensemble sur la zoologie du Congo Belge. *I.R.S.A.C. Rapport Annuel* **1**, 87–158.

Schumacher, S. (1918). Bau der ausseren Haut eines Fetus von *Hippopotamus amphibius* Linn. *Anat. Anz.* **51**, 156–173.

Schütte, G. W. (1973). Hippopotamus behaviour after shooting an adult female. *Lammergeyer* **19**, 36.

Schwarz, E. (1933). Der Gattungsname des Afrikanischen Flusschweines. *Z. Säugetierk.* **8**, 284.

Sclater, P. L. (1861). Note on the reproduction of the red river hog (*Potamochoerus pencillatus*) in the Society's menagerie. *Proc. Zool. Soc. London* **1861**, 62–63.

Sclater, P. L. (1901a). A new mammal. *Proc. Zool. Soc. London* **1**, 3–6.

Sclater, P. L. (1901b). On an apparently new species of zebra from the Semliki Forest. *Proc. Zool. Soc. London* **1**, 50–52.

Sclater, P. L. (1904a). The forest pig of Central Africa. *Nature, London* **27** (10), 626.

Sclater, P. L. (1904b). On the okapi. *Proc. Zool. Soc. London* **2**, 180.

Scotcher, J. S. B. (1973a). Observations on the breeding behaviour of hippopotamus. *Lammergeyer* **19**, 35–36.

Scotcher, J. S. B. (1973b). Diurnal feeding by bushpigs. *Lammergeyer* **19**, 33.

Senior, M. and Tong, E. H. (1963). Parturition in a hippopotamus. *Proc. Zool. Soc. London* **140**, 57–59.

Shalash, M. R. and Nawito, M. (1964). Some reproductive aspects in the female camel. *Int. Congr. An. Reprod. A.I.* **2**, 263–273.

Shaw, J. C. M. (1939). Growth changes and variation in warthog third molars and their palaeontological importance. *Trans. Roy. Soc. S. Afr.* **27**, 51–94.

Sidney, J. (1965). The past and present distribution of some African ungulates. *Trans. Zool. Soc. London* **30**, 1–396.

Siebert, B. D. and MacFarlane, W. V. (1971). Water turnover and renal function of dromedaries in the desert. *Physiol. Zool.* **44**, 225–240.

Signoret, J. P. and Dumesnil Du Buisson, F. (1961). Etude du comportement de la truie en oestrus. *C.R. 4e Congr. Int. Reprod. Anim. (La Haye).* 171–175.

Simon, N. (1962). "Between the Sunlight and the Thunder." Collins, London.

Simpson, C. D. (1964). Observations on courtship behaviour in warthog (*Phacochoerus aethiopicus*) Pallas. *Arnoldia, Rhodesia* **1** (20), 1–4.

Simpson, G. G. (1945). The principle of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* **85**, 1–350.

Simpson, G. G. (1963). Mammalian evolution on the southern continents. *Proc. XVI Int. Congr. Zool. Washington* **4**, 63–65.

Singer, R. and Boné, E. L. (1960). Modern giraffes and the fossil giraffids of Africa. *Ann. S. Afr. Mus.* **45**, 375–548.

Singh, V. and Prakash, A. (1964). Mating behaviour in camel. *Ind. Vet. J.* **41**, 475–477.

Skinner, J. D., Breytenbach, G. J. and Maberly, C. T. A. (1976). Observations on the ecology and biology of the bush pig *Potamochoerus porcus* Linn. in the northern Transvaal. *S. Afr. Wildl. Research J.* **6** (2), 123–128.

Slijper, E. J. (1956). Some remarks on gestation and birth in aquatic mammals. *Hvalrad Skr.* **41**, 1–62.

Slijper, E. J. (1968). On the heart of temporary aquatic mammals with special reference to the embryonic pathways. *Bijdr. Dierk.* **38**, 75–84.

Smithers, R. H. N. (1966). "The Mammals of Rhodesia Zambia and Malawi." Collins, London.

Sowls, L. K. (1974). Social behaviour of collared peccary (*Dicotyles tajacu*). *In* "The Behaviour of Ungulates and its Relation to Management." (Geist, V. and Walther, F. eds), TUCN Publ. 24.

Sowls, L. K. and Phelps, R. J. (1966). Body temperature of juvenile warthogs and bushpigs. *J. Mammal.* **47** (1), 134–137.

Speight, W. L. (1948). Mouse deer (chevrotain). *Afr. Wildlife Johannesburg* **21**, 25–28.

Spencer, P. (1973). "Nomads in Alliance." Oxford University Press, Oxford.

Spinage, C. A. (1968a). Horns and other bony structures of the skull of the giraffe and their functional significance. *E. Afr. Wildl. J.* **6**, 53–61.

Spinage, C. A. (1968b). "The Book of the Giraffe." Collins, London.

Spinage, C. A. (1972). African ungulate life table. *Ecology* **53**, 645–652.

Spinage, C. A., Guinness, F., Eltringham, S. K. and Woodford, M. H. (1972). Estimation of large mammal numbers in the Akagera National Park and Mutara Hunting Reserve Rwanda. *Terre et Vie* **4**, 564–570.

Stanton, J. (1955). Is the giraffe mute? *Nat. Hist.* **64**, 128–129.

Stevenson-Hamilton, J. (1947). "Wildlife in South Africa." Cassel, London.

Stockley, C. H. (1952). Giant forest hog. *Country Life London* **112**, 341–342.

Stott, K. (1959). Giraffe intergradation in Kenya. *J. Mammal.* **40**, 251.

Swank, G. W. and Petrides, G. A. (1957). Hippopotamus population densities in Queen Elizabeth National Park and the effects of a local reduction in their numbers. Fulbright Programme, Entebbe, Uganda. Game and Fisheries Dept. Mimeo.

Tanaka, Jiro (1976). Report on camel herders in northern Kenya. *Sizen*, April.

Thenius, E. (1950). *Postpotamochoerus* nov. subgen. *Hyotheroides* aus dem Unter Pliozän von Samos and die Herkunft der Potamochoeren Sitz. Österr. *Akad. Wiss. Math. Math. Natw. K. Wien* **1**, 159, 25–35.

Thenius, E. (1962). Die Grossäugetiere des Pliozänes von Mitteleuropa. *Z. Säugetierk.* **27**, 65–83.

Thenius, E. (1969). "Phylogenie der Mammalia. Stemmesgeschichte der Säugetiere (einschliesslich der Hominiden)." De Gruyter, Berlin.

Thenius, E. (1970). Zur Evolution und Verbreitungsgeschichte der Suidae (Artiodactyla, Mammalia). *Z. Säugetierk.* **30**, 367–380.

Thenius, E. (1972). "Grundzüge der Verbreitungsgeschichte der Säugetiere. Eine historische Tiergeographie." Fischer, Stuttgart.

Thenius, E. and Hofer, H. (1967). "Die Giraffen und ihre Vorfahren." Kosmos, Stuttgart.

Thomas, A. D. and Kolbe, F. F. (1942). The wild pigs of South Africa. Their distribution and habits and their significance as agricultural pests and carriers of disease. *J. S. Afr. Vet. Med. Ass.* **13**, 1–11.

Thomas, O. (1904). On *Hylochoerus* the forest pig of Central Africa. *Proc. Zool. Soc. London* **1904** (2), 193–199.

Thurlbeck, W. M. (1965). Arteriosclerosis in hippopotami. *In* "Comparative arteriosclerosis" (Roberts, J. C. and Strauss, S. eds), Harper and Row, New York.

Thurston, J. P. (1963). Schistosomes from *Hippopotamus amphibius* Linn. I. The morphology of *Schistosoma hippopotami* sp. nov. *Parasitology* **53**, 49–54.
Thurston, J. P. (1964). Schistosomes from *Hippopotamus amphibius* II. The morphology of Schistosoma edwardiense sp. nov. *Parasitology* **54**, 67–72.
Thurston, J. P. (1968a). The larva of *Oculotrema hippopotami*. *J. Zool. London* **154**, 475–480.
Thurston, J. P. (1968b). The frequency distribution of *Oculotrema hippopotami* on *H. Amphibius*. *J. Zool. London* **154**, 481–485.
Thurston, J. P. and Grant, J. (1971). Holotrich ciliates from the stomach of *Hippopotamus amphibius* with descriptions of two new genera and four new species. *J. Protozool.* **18**, 133–141.
Thurston, J. P. and Laws, R. M. (1965). Oculotrema hippopotami in Uganda. *Nature, London* **205**, 1127.
Thurston, J. P., Noirot-Timothée, C. and Arman, P. (1968). Fermentative digestion in the stomach of *Hippopotamus amphibius* and associated ciliate protozoa. *Nature, London* **218**, 882–883.
Toldt, K. (1919). Neuere Arbeiten über das Integument des Flusspferdes. *Biol. Zbl.* **39**, 346–351.
Toldt, K. (1932). "Natürliche Färbungen bzw. Zeichnungen der Säugetierhaut." Leipzig.
Tookey, E. B. (1958). Pigs. *Wildlife Nairobi* **1** (2).
Torry, W. I. (1973). Subsistence ecology among the Gabra: Nomads of Kenya/Ethiopia frontier. Ph.D. Thesis Columbia.
Turnbull, C. M. (1961). "The Forest People." Jonathan Cape, London.
Turner, M. (1969). Letter and photograph to Africana. *Africana* **1969**.
U.G.R. (1929). Reports of the Uganda Game Department 1929.
Ullrich, W. (1955). Vom okapi. *Urania* **18**, 222–225.
Urbain, A., Nouvel, J. and Bullier, P. (1944). Neoformations cutanées et osseuses de la tête chez les girafes. *Bull. Mus. Hist. Nat. Paris* **2** (16), 91–95.
Urbain, A. and Rode, P. (1948). Un okapi au Zoo de Vicennes. *Mammalia* **12**, 45–46.
Vandermander, A. (1953). Aperçu succinct de nos connaissances actuelles au sujet de l'okapi. *Bull. Soc. Roy. Zool. Anvers* **3**, 22–44.
Verheyen, R. (1951). "Contribution à l'étude éthologique des mammifères de Parc National de l'Upemba." Inst. Parcs Natn. Congo Belg., Brussels.
Verheyen, R. (1954). Monographie éthologique de l'hippopotame (*Hippopotamus amphibius*) Linn *Éxplorat. Parcs Natn. Albert*, 1–91. Inst. Parcs Natn. Congo Belge, Brussels.
Verschuren, J. (1958). Ecologie et biologie des grands mammifères. *Éxplorat. Parcs Natn. Garamba*. Inst. Parcs Natn. Congo Belge, Brussels.
Vesey-Fitzgerald, D. F. (1954). Ordeal by drought. *Field, London* **203**, 351.
Vesey-Fitzgerald, D. F. (1960). Grazing succession among East African game animals. *J. Mammal.* **41**, 161–172.
Viret, J. (1961). Artiodactyla. *In* "Traité de Paléontologie." Vol. 6, pp. 887–1104. Masson et Cie, Paris.
Waddington, C. H. (1953). The evolution of adaptations. *Endeavour* **12**.

Walker, E. P. (1964). "Mammals of the World." John Hopkins Press, Baltimore.
Walther, F. (1959). "Antilopenhafte" Verhaltenweisen in Paarungzeremoniell des Okapi. *Z. Tierpsychol.* **17**, 180–210.
Walther, F. (1961). The mating behaviour of certain horned ungulates. *Int. Zoo Yearbook* 3.
Walther, F. (1962). On play behaviour in *Okapia johnstoni*. *Z. Säugetierk.* **27**, 245–251.
Walther, F. (1967). Territorial and marking behaviour in ungulates. *In* "Die Strassen der Tiere." (Hediger, H. ed.), Vieweg Publ.
Walther, F. (1974). Some reflections on expressive behaviour in combat and courtship of certain horned ungulates. *In* "The Behaviour of Ungulates and its Relation to Management," (Geist, V. and Walther, F. eds.), IUCN Publ. 24.
Watson, R. M., Graham, A. D. and Parker, I. S. C. (1969). A census of the large mammals of Loliondo controlled area Northern Tanzania. *E. Afr. Wildl. J.* **7**, 43–59.
Webb, S. D. (1972). Locomotor evolution in camels. *Forma et Functio* **2**, 99–111.
Western, D. (1971). Giraffe chewing a Grant's gazelle carcasse. *E. Afr. Wildl. J.* **9**, 156–157.
White, T. D. and Harris, J. M. (1977). Suid evolution and correlation of African hominid localities. *Science* **198**, 13–21.
Whittow, G. C. (1971). Ungulates. In: Whittow. Comparative physiology of thermoregulation Vol. II, 191–281. Academic Press, London and New York.
Willemse, J. (1962). An impudent bushpig. *Fauna and Flora, Pretoria* **13**, 54.
Winton, W. E. de (1897). Remarks on the existing forms of giraffe. *Proc. Zool. Soc. London* 273–283.
Wissmann, V. and Kuhnert, W. (1908). "In der Wildkammer Afrikas und Asien." Berlin.
Wodzicki, K. A. (1950). Wild pig, *Sus scrofa*, Linn. *New Zealand DSIR Bull.* **98**.
Woodhouse, C. W. (1911). Some East African pigs. *J. E. Afr. Uganda Nat. Hist. Soc.* **2** (3), 40–42.
Woods, T. D. (1972). Pre-copulatory behaviour in male giraffe. *Lammergeyer* **17**, 67.
Wright, P. C. (1964). Wild animals in the tropics. *In* "The Biology of Survival." Symp. Zool. Soc. London No. 13. (Edholm, O. G. ed.), pp. 17–28. Academic Press, London and New York.
Wyatt, J. R. (1969). The feeding ecology of giraffe (*Giraffa camelopardalis*) in Nairobi National Park and the effect of browsing on their main food plants. M.Sc. Thesis. University of East Africa. Nairobi.
Wyatt, J. R. (1971). Osteophagia in Masai giraffe. *E. Afr. Wildl. J.* **9**, 157.
Young, J. Z. (1962). "The Life of Vertebrates." Clarendon Press, Oxford.
Zukowsky, L. (1921). Mitteilungen uber ein anscheinend neue form von *Hylochoerus* aus dem Winterhochlande von Mutjekgebirge und vom Meru-Berge. *Arch. Naturgeschich.* **87**, 179–191.

Systematic Index

A

Aceratherium 82
Anchitherium 121
ant 311, 325
antelope 180, 263
  pigmy 180
anthracothere 15, 250
Anthracotheriidae 183
Archaeohippus 121
Archaeomeryx 180
artiodactyl 4, 78 *et seq.*
Artiodactyla 180, 200, 210, 230, 256, 298, 339
ass 125, 139, 143
  African 129
  Somali 135

B

bongo 222 *et seq.*
Boselaphus 310
botfly 178
bovid 2, 127, 180 *et seq.*
Bovidae 78, 183
Brachypotherium 82
Bramatherium 311
brontothere 78
buffalo 109, 140, 224 *et seq.*
Bunolistriodon 185
bushpig (river hog, *Potamochoerus porcus*) 180 *et seq.*

C

Caenopus 82, 83
camel 4, 78, 278 *et seq.*
  Bactrian 289
  dromedary (*Camelus dromedarius*) 280, 281
camelid 182
Camelidae 278, 280
Camelus 180, 183, 281
  dromedarius 280, 281
  thomasi 281
cat 208
Ceratomorpha 80
ceratomorph 80
Ceratotherium 78 *et seq.*
  praecox 83
  simum 83, 106 *et seq.*
Cervoidea 183
chalicothere 1, 78
cheetah 175, 248
chevrotain 1, 4, 78, 180, 181, 294 *et seq.*
  water (*Hyemoschus aquaticus*) 298, 299
chimpanzee 304
Choeropsis 250 *et seq.*
  liberiensis 252
Coelodonta 82
Colobus abyssinicus 68
condylarth 77
Connochaetes taurinus 140
Crematogaster 311, 325
crocodile 65, 103, 337

D

deer 78, 296
Diceratherium 77
Dicerorhinus 80 *et seq.*
Diceros 78 *et seq.*
  bicornis 92 *et seq.*
  pachygnathus 82, 83
Dictylocaulus 178
dog, wild 174, 175, 226, 249
Dolichohippus 128
donkey 143
Dorcatherium 297
dromedary (*Camelus dromedarius*) 281
dugong 15, 234
duiker 180, 304
Dyseotylopus 278

E

eagle 208
  martial 249
elephant 1 *et seq.*
  African (*Loxodonta africana*) 12 *et seq.*
  Asiatic 54

bush (savanna, *Loxodonta a. africana*) 31
dwarf 12
forest (*Loxodonta africana cyclotis*) 25, 27, 31
savanna (bush, *Loxodonta a. africana*) 25, 31
elephantid 18 *et seq.*
Elephantidae 17 *et seq.*
Elephas 16, 19 *et seq.*
antiquus 29
celebensis 20, 21
ekorensis 20
falconeri 12, 26, 29
hysudricus 12, 20
hysudrindicus 20
indicus 24, 27
iolensis 25
maximus 19, 20
mnaidriensis 12
namadicus 12
group 20
planifrons 11, 12, 20, 23
platycephalus 20
recki 20, 24
Entelodontidae 183
Eohippus 121
Epiphippus 121
equid 76, 79, 120 *et seq.*
Equidae 76, 78, 120, 146, 163
Equus 77, 78, 120 *et seq.*
asinus 125, 126, 143
× *E. zebra* 138
hemionus × *E. quagga burchelli* 138
caballus 125, 126, 129, 138 *et seq.*
× *E. quagga boehmi* 138
× *E. q. quagga* 138
przewalskii 131, 138
feras 138
grevyi 125 *et seq.*
× *E. zebra* 138
johnstoni 339
laurentius 138
plicatus 127, 147
quagga 120, 125 *et seq.*
antiquorum 147, 164 *et seq.*
boehmi 130, 138 *et seq.*
× *E. caballus* 138
burchelli 164 *et seq.*
× *E. asinus hemionus* 138
chapmani 166
crawshayi 163 *et seq.*
quagga 138 *et seq.*
× *E. caballus* 138
selousi 164, 165
wahlbergi 166
sanmeniensis 126, 127, 147
scotti 138
sellardsi 127
simonescui 138
simplicidens 123
sivalensis 127
valeriani 138, 147
zebra 130, 134, 140, 151
× *E. asinus* 138
× *E. grevyi* 138

G

Gazella thomsoni 140
Giraffa 183
camelopardalis 310, 323
angolensis 317, 320
camelopardalis 317 *et seq.*
congoensis 317, 318
"*cottoni*" 313, 320
giraffa 317 *et seq.*
peralta 317 *et seq.*
reticulata 313 *et seq.*
rothschildi 313 *et seq.*
thornicrofti 317
tippelskirchi 312 *et seq.*
× *reticulata* 320
gracilis 308, 310
jumae 308, 310
giraffe (*Giraffa camelopardalis*) 1, 4, 7, 141, 157, 180 *et seq.*
Angolan 320
Galana hybrid 317
Masai (*Giraffa camelopardalis tippelskirchi*) 319 *et seq.*
Nubian 320
reticulated 320
Rothschild's/Baringo 317, 320
southern 320
Ugandan 320
West African 320

giraffid 182, 308 *et seq.*
Giraffidae 183, 308, 313, 339
gnu 168, 174
goat 273
gomphothere 20, 21, 24
Gomphotherium 9, 11, 16, 20, 22
angustidens 15, 23

H

hartebeest 175
Helogale 69
Hipparion 120, 123
hippo 250 *et seq.*
diprotodont 251
hexaprotodont 251, 253
tetraprotodont 251
hippopotamid, 182, 250
Hippopotamidae 183, 250, 252, 256
hippopotamus (*Hippopotamus amphibius*) 1, 2, 4, 6, 78, 103, 180, 238, 250 *et seq.*
pigmy 15, 180, 250
Hippopotamus 183
amphibius 250 *et seq.*
gorgops 251, 253, 254
imagunculus 253
karumensis 251, 253
lemerlei 253
protamphibius 251, 253
"hippotigris" 147
hog, giant (*Hylochoerus meinertzhageni*) 180, 185 *et seq.*
river (bush pig, *Potamochoerus porcus*) 200, 201
Homacodon 180
hominid 18
hookworm, liver 344
horse 76, 81, 120 *et seq.*
caballine 123, 138
dawn 121
domestic 138
Magdalenian 135
Miocene 77
Przewalski 135
hyaena 65 *et seq.*
Hyaena hyaena 135
Hydracodontidae 81
Hyemoschus 180, 183, 297 *et seq.*
aquaticus 296 *et seq.*
hylochoere 196
hylochoerine 194
Hylochoerus 183 *et seq.*
meinertzhageni 210, 211
Hypohippus 121
Hyrachidae 81
hyracoids 15
Hyracotherium 76, 77, 78, 121, 123
hyrax 79, 98

J

jackass 131, 143

K

kangaroo, marsupial 125
kongoni 140

L

lagomorph 79
leopard 208, 248, 249, 337, 344
Leptomeryx 180
Libytherium 308
lion 58 *et seq.*
loxodont 25
Loxodonta 10, 13, 16, 23 *et seq.*
adaurora 11, 12, 20 *et seq.*
africana 9, 11, 20 *et seq.*
africana 25, 27, 30 *et seq.*
cyclotis 12, 25 *et seq.*
atlantica 20, 25
Lycaon 7, 226
Lyperosica 103

M

mammal 1 *et seq.*
mammoth 23
Mammut 16
Mammuthus 16, 19, 24
africanavus 20
imperator group 20
meridionalis 20, 23
primigenius 19, 20
subplanifrons 20
man 2
Manodontella 344
mastodont 17
Megahippus 121
Merychippus 121, 123
(*Protohippus*) 122
republicans 126

Merycopotamus dissimilis 253
mesochoere 196
Mesochoerus 185, 186, 194 *et seq.*
  limnetes 185, 194, 195
  majus 185
Mesohippus 121, 122
Metamynodon 254
Metridiochoerus 185, 191
  andrewsi 185, 192
  hopwoodi 185
  jacksoni 192
  modestus 185
Miohippus 77, 121
Moeritherium 15
mule 143
Mungos 69

N

Neohipparion 121
nilghai 310
notochoerine 191
Notochoerus 185, 191, 192
  capensis 185, 192
  euilus 185
notoungulate 125
Nyanzochoerus 195
  jaegeri 185, 191
  kanamensis 185
  tulotes 185, 192

O

okapi (*Okapia johnstoni*) 135, 180, 182, 308, 311, 339 *et seq.*
Okapia 183
  johnstoni 338, 339
oreodont 78
Ornithodorus moubata 249
Orohippus 121
Orycteropus 188, 223, 234 *et seq.*
oxen 180

P

Palaeochoerus 185
Palaeodonta 183
Paradiceros mukiri 82, 83
Parahippus 121, 123
Parascaris 178
peccary 250, 251, 253
Perchoerus 253
perissodactyl 76 *et seq.*
Perissodactyla 76, 92, 106, 146, 163
Phacochoerus 183 *et seq.*
  aethiopicus 192, 230, 231, 236
  africanus 192
  antiquus 192
Phenacodus 76, 77
  primaevus 76
Phiomia 9, 10, 15
  minor 15
pig 1, 4, 5, 15, 78, 180 *et seq.*
  phacochoerine 191, 235
Pliohippus 121
  perix 126
Poebrodon 278
Poebrotherium 180, 278
Poliaomaetus bellicosus 249
potamochoerine 194
Potamochoerus 183 *et seq.*
  porcus 200, 201
    larvatus 201
    porcus 201
Primelephas 16, 21
  gomphotheroides 20 *et seq.*
proboscid 8 *et seq.*
Proboscidea 8 *et seq.*
Procamelus 279
Protapir validus 15
puku 263
python 65, 298

Q

quagga 132, 166
  Cape 135, 138, 139, 166
  painted (common zebra, *Equus quagga*) 163

R

rhino 7, 66, 78 *et seq.*
rhinoceros (*Diceros bicornis*) 3, 4, 5, 76 *et seq.*
  African 80 *et seq.*
  black (*Diceros bicornis*) 77, 92 *et seq.*
  browse (*Diceros bicornis*) 92, 93
  grass (white, *Ceratotherium simum*) 78,106 *et seq.*
  great Indian 81

Indian 81
Miocene 77
white (grass, *Ceratotherium simum*) 86, 106 *et seq.*
woolly 82
Rhinoceros 80, 81
rhinocerotid 79
Rhinocerotidae 76, 80, 92, 106
Rhinomusca 103
rodent 79
ruminant 182

S

shrew 1
sirenian 15
Sivatherium 311
Stegodibeledon 21
stegodon 16
Stegodon 16
ganesa 17
stegodont 17
Stegomastodon 16
Stegotetrabelodon 9 *et seq.*
lybicus 20, 21
orbus 20, 21, 23
schneideri 21
syrticus 15, 21
Stephanofilaria dinniki 103
Strongylus vulgaris 178
subungulate 15
suid 182, 235
Suidae 183, 184, 200, 210, 230
Sus 185, 229
Syncerus caffer 140

T

tapeworm 178
tapir 8, 15, 76, 77, 81, 121
Tapiroidea 79
Tapirus 77
Tayassu 250
tick 103, 249
topi 140
tragulid 76, 121, 180, 182, 295
Tragulidae 295, 298
Traguloidea 183
Tragulus javanicus 300, 304
memnina 299 *et seq.*
Trichinella 223
Trigonias 82
tylopod 278
Tylopoda 183, 278

U

ungulate 4, 78, 120, 198, 224, 332
Uranomys 234

W

warthog (*Phacochoerus aethiopicus*) 5, 109, 180, 188 *et seq.*
water buffalo 15
waterbuck 263

Z

zebra 2, 7, 68, 125 *et seq.*
Burchell's 132, 166
common (painted quagga, *Equus quagga*) 129 *et seq.*
Grevy's (Somali zebra, *Equus grevyi*) 129 *et seq.*
"hippotigrine" 128
Somali (Grevy's zebra, *Equus grevyi*) 146, 147

Subject Index

A

Abortion,
  elephant 70
Activity, nocturnal,
  bushpig 205
  camel 287
  giant hog 213
  hippo 260
  warthog 236, 238
  zebra, common 170
Activity patterns,
  bushpig 205, 206
  camel 286 *et seq.*
  chevrotain 300
  elephant 47, 48
  giant hog 212, 213
  giraffe 325, 329
  hippo 260
  okapi 240
  rhino 88, 95
  Tragulus javanicus 300
  warthog 235, 238, 239
  zebra, common 170
Adaptation, 5
  artiodactyl 180 *et seq.*
  camel 281 *et seq.*
  chevrotain 296, 297
  equid 121, 123
  giraffe 308 *et seq.*
  hippo 250 *et seq.*
  Tapiroidea 79
Adaptation, ecological,
  suid, 184
Adolescence, 3
Adulthood, 3
Age distribution,
  elephant 55
Age estimation,
  elephant 18
Ageing,
  hippo 259
Aggression, 7
  camel 289
  elephant 52 *et seq.*
  equid 130
  hippo 262, 267 *et seq.*
  zebra, common 170, 172
Albinism,
  giraffe 316, 321
  hippo 260, 261
Ancestry,
  caballine horse 138
  hippo 253
  perissodactyl 76
  proboscid 15, 17
Articulation, skull and jaw,
  hippo 254
Associations,
  Connochaetes taurinus 140
  Equus grevyi 141
    quagga 140, 141
  Gazella thomsoni 140
  giraffe 141
  Syncerus caffer 140
  zebra, common 178
Astralagus,
  artiodactyl 181

B

Bachelor group,
  camel, Bactrian 289
  equid 132
  giraffe 310, 333
  hippo 266
  zebra, common 131, 172
    Grevy's 131
Balance,
  camel 281, 282
  elephant 12, 14
Basisphenoid,
  elephant 11
Bathing,
  elephant 47
  hippo 260 *et seq.*
Behaviour, 3
Bioenergetics, 3
Birth,
  bushpig 208
  camel 291
  elephant 70, 71

giant hog 227
giraffe 335
hippo 275
rhino 102
warthog 243, 246
zebra, common 178
Birth frequency,
camel 291
elephant 71
giraffe 337
zebra, common 176
Blood,
camel 286
Blood pressure regulation,
giraffe 313
Brain,
elephant 11
Elephas hysudricus 12
Proboscidea 14
Breeding,
bushpig 208
camel 289
chevrotain 304 *et seq.*
elephant 68 *et seq.*
giant hog 226 *et seq.*
giraffe 333, 335
hippo 273 *et seq.*
okapi 342 *et seq.*
rhino, black 90, 101, 102
white 117
warthog 243, 246 *et seq.*
zebra, common 173 *et seq.*
Grevy's 150 *et seq.*
Breeding season,
bushpig 208
camel 290
chevrotain 304
elephant 68
hippo 267, 273, 275
rhino 90, 91
black 101
white 117
Tragulus javanicus 304
warthog 243
zebra, common 176
Grevy's 150, 151
Browsing zone,
giraffe 308
okapi 308
Bunching,
zebra, Grevy's 156, 157
Burial ceremony,
elephant 58, 59
Bush thrashing,
elephant 59

C

Caecum,
elephant 38
Equus 78
Callosities,
warthog 234
Camouflage,
giraffe 319, 322
Captivity, success in,
giraffe 337
hippo 272
Hylochoerus 229
okapi 344
rhino, black 91
white 118
Cave paintings,
giraffe 337
horse 132, 139
rhino, Black 86
White 107
Characteristics,
artiodactyl 181 *et seq.*
bushpig 201
camel 281, 282
ceratomorph 80 *et seq.*
chevrotain 299
elephant 31
equid 121 *et seq.*
Equus grevyi 147
quagga 165 *et seq.*
Giant hog 211
giraffe 313, 316
hippo 257, 259
hippopotamid 251 *et seq.*
okapi 339
perissodactyl 76 *et seq.*
pig 185 *et seq.*
warthog 231, 232
Cheek shield,
Notochoerus capensis 192
Potamochoerus 194
Chewing (*see also* Mastication)

giant hog 196
gomphothere 20, 21
Chewing the cud,
Giraffa 183
Chromosome number,
Ceratotherium 83
Diceros 83
Claws, 4
Climatic changes, 16, 29, 42
Clitoris,
elephant 69
Coat pattern (*see also* Stripes)
ass, Somali 135
bongo 342
bovid 342
Cape quagga 135
chevrotain 299
equid 131 *et seq.*
Equus grevyi 131 *et seq.*
young 154
× *E. zebra* 138
quagga 136 *et seq.*
antiquorum 164 *et seq.*
boehmi 164 *et seq.*
× *E. caballus* 138
burchelli 164 *et seq.*
× *E. asinus hemionus* 138
crawshayi 164 *et seq.*
selousi 164 *et seq.*
quagga 164 *et seq.*
× *E. caballus* 138
zebra × *asinus* 138
Giraffa camelopardalis angolensis 320
camelopardalis 320, 322
cottoni 320
giraffa 317, 320, 321
peralta 320 *et seq.*
reticulata 317, 320, 322
× *G. c. tippelsikirchi* 320
rothschildi 320
tippelsikirchi 317 *et seq.*
giraffe 316 *et seq.*
horse, Magdalenian 135
Przewalski 135
Hyaena hyaena 135
okapi 135, 341 *et seq.*
Coat pattern development,
chevrotain 299
Equus grevyi 140
quagga 140
zebra 140
Giraffa camelopardalis reticulata 318
giraffe 318, 321
Colour mutant,
giraffe 321
Communication,
chevrotain 299
elephant 62
giraffe 326
rhino, African 87, 88
Community, 1, 2
Competitors, 1, 3, 4
Competition,
camel 286
chevrotain 304
elephant 44, 66
elephantid 25, 87
equid 127
giant hog 185, 224
Hylochoerium 198
perissodactyl 78
rhino, Black 87, 103
warthog 185
zebra, common 172
Competition, intraspecific, 4, 10
bushpig 207
chevrotain 302, 304
giant hog 211, 228
giraffe 311
hippo 250
Hylochoerium 198
rhino 90
Conservation, 2, 7
elephant 75
rhino, white 118, 119
zebra, Grevy's 161
Convergence (*see* Evolution, convergent)
Copulation (*see* Mating)
Corpora lutea,
elephant 69, 70
Courtship,
bushpig 208
camel 290
chevrotain 304
elephant 69

giant hog 226
giraffe 335
hippo 275
horse 133
okapi 342 *et seq.*
rhino 90
black 101, 102
white 117
warthog 246
zebra, common 177
Grevy's 152
"Covering" behaviour,
elephant 45, 46
Cranium,
elephant 12
Elephas 24
namadicus 12
Hippopotamidae 252, 254
Loxodonta 24
Mammuthus 24
proboscid 11
Cranium pneumatization,
elephant 34
Proboscidea 11
Cultural importance,
zebra 179

D

Damage caused,
bushpig 202, 209
zebra 143
Defaecation,
Equus caballus 170
hippo 263
zebra, common 170, 177
Defence, 5, 6
bushpig 209
Ceratotherium 89
chevrotain 301
elephant 53, 57, 58, 64, 65
giant hog 226
giraffe 311, 337
hippo 267, 273
okapi 344
rhino 81
black 102
warthog 248, 249
zebra, common 174, 175
Grevy's 157
Dentition 18 (*see also* Teeth)
bushpig 201
elephant 21, 24
hippo 253, 259
Hyemoschus 304
Merychippus 123
Phenacodus 76
Potamochoerus 185
Diastema,
Archaeomeryx 180
artiodactyl 180, 181
Camelus 180
Hyemoschus 180
Homacodon 180
Poëbrotherium 180
Diet,
Ceratotherium 78
equid 121
Equus grevyi 148
hippo 261
hylochoere 196
Hylochoerus 186
perissodactyl 78, 79
proboscid 16
Digestion,
artiodactyl 78, 182
bovid 127
equine 125, 127
hippo 250, 261, 262
perissodactyl 78
Digging,
bushpig 201, 202, 205
giant hog 214, 215
rhino 95
warthog 235
Disease,
bushpig 208
elephant 66
giant hog 222, 223
hippo 273
rhino, black 103
warthog 249
zebra, common 178
Disease, resistance to,
hippo 273
rhino 87
black 103
Dispersal, 4
chevrotain 304

elephant 48 *et seq.*
Equus grevyi 154 *et seq.*
hippo 264
rhino 93
Display, 7
bushpig 206
camel 290
elephant 34, 58 *et seq.*
giraffe 329
hippo 269, 271
rhino, black 97, 101, 102
White 112, 115
warthog 242
zebra, common 170, 172
Display, intimidation,
elephant 58 *et seq.*
Disposition,
chevrotain 303, 304
elephant, African 54
Asiatic 54
Equus grevyi 154
hippo 272
horse 131
jackass 131
okapi 341
rhino, black 103
White 109, 118
Dissection
warthog piglet 245
Distribution,
bushpig 224
camel 281, 293
chevrotain 299, 300, 304
Diceros bicornis 93, 94, 105
Elephas indicus 24, 27
mnaidriensis 12
namadicus 12
recki 24
equid 121
Equus grevyi 147 *et seq.*
quagga 160, 166 *et seq.*
antiquorum 147, 165
boehmi 165
burchelli 165
crawshayi 165
quagga 165
selousi 165
Giant hog 212, 224
Giraffa camelopardalis angolae 320
angolensis 317
camelopardalis 317 *et seq.*
congoensis 317 *et seq.*
cottoni 320
giraffa 317, 320
peralta 317 *et seq.*
reticulata 313, 317 *et seq.*
rothschildi 313, 317 *et seq.*
thornicrofti 317
tippelskirchi 313, 317 *et seq.*
× *G. c. reticulata* 320
giraffe 316 *et seq.*
Galana hybrids 317
Rothschild/Baringo 317
Hippopotamus 264 *et seq.*
Hylochoerus 189, 213
Loxodonta africana 40, 41, 48, 73
cyclotis 27
Okapia johnstoni 339, 340, 345
perissodactyl 76
Phacochoerus 189
aethiopicus 231, 234 *et seq.*
Potamochoerus 189, 201, 202
rhino 86
white 107 *et seq.*
warthog 224
zebra 143
Domestication,
camel 281
giant hog 229
Dominance,
bushpig 207
camel 289
equid 130
Equus grevyi 149, 151, 152
giraffe 327, 331, 332
hippo 262
rhino 80, 89
black 101
white 112, 115, 116
warthog 242
Drinking, 4
camel 286, 287
elephant 36, 47
giant hog 217
giraffe 326
rhino, black 90, 93, 95
white 110
warthog 238

zebra, common 170
Drought,
Diceros 87
elephant 72
Equus grevyi 147
hippo 261, 273
rhino 87
Dung,
elephant 46
giant hog 214, 217
hippo 262
warthog 214, 215
Dung eating,
hippo 263
rhino 95
warthog 238
Dung marking,
giant hog 216
hippo 263, 266
rhino, black 98
white 110
Dung middens,
bushpig 208
Ceratotherium 88
Equus grevyi 151
giant hog 215
hippo 263
rhino, black 98
white 110

E

Ear,
Loxodonta africana 34
africana 34
cyclotis 34
Ear signalling,
Equus grevyi 157
Ecological community,
rhino 93
Ecological conditions,
elephant 42, 43
Ecological niche, 1, 2
anthracothere 253
artiodactyl 183
Ceratotherium 84
equid 121, 128
giraffe 308
hippo 250, 253
Hyracotherium 76
Loxodonta africana 25, 26, 29
perissodactyl 78, 79
Potamochoerus 185
Proboscidea 8, 15
rhino, black 93, 105
Economic importance,
camel 292, 293
Ecosystem, effect,
equid 128, 129
giraffe 325
Loxodonta africana 43
Enamel,
Gomphotherium angustidens 23
Loxodonta africana 23
Primelephas gomphotheroides 23
proboscid 20
Stegotetrabelodon orbus 23
Energy flow, 3
Environment, 1, 4
Environment, effect,
elephant 43, 66, 73
hippo 264, 266
Evolution, 3 *et seq.*
artiodactyl 180 *et seq.*
Camelidae 278, 279
chevrotain 295 *et seq.*
Elephas 12
giraffid 308, 313, 318 *et seq.*
hippo 250 *et seq.*
horse 120 *et seq.*
perissodactyl 76 *et seq.*
Proboscidea 8 *et seq.*
suid 184 *et seq.*
warthog 235
Evolution, convergent,
hippo 253
Merycopotamus 253
proboscid 15, 17
tapir 15
Evolution, parallel,
equid 121
proboscid 17
Extinction, 2, 3
Dicerorhinus 81
Elephas antiquus 29
falconeri 29
Loxodonta africana 40, 41
rhino 87
Eye,
elephant 62

F

Facial pattern,
artiodactyl 182
bushpig 201, 206
okapi 342
zebra 124
Grevy's 157
Family unit,
bushpig 207
elephant 52 *et seq.*
giant hog 217
giraffe 326
hippo 267
horse 130 *et seq.*
warthog 240, 243, 247
zebra 130 *et seq.*
common 172 *et seq.*
Feeding,
camel 286 *et seq.*
elephant 40 *et seq.*
giant hog 214 *et seq.*
giraffe 308 *et seq.*
hippo 259, 260, 263
Hylochoerus 186
perissodactyl 78
Proboscidea 8 *et seq.*
rhino 78, 82
warthog 235 *et seq.*
zebra, common 168
Femur,
elephant 14
Fertility,
camel 292
Fertility rate,
warthog 246
Fighting, 4 *et seq.*
bushpig 194, 195, 206
camel 282, 289, 290
chevrotain 302 *et seq.*
Dicerorhinus 81
Diceros 87, 97, 101
elephant 34, 59 *et seq.*
Equus caballus 170
grevyi 150, 152, 157
giant hog 211, 212, 228, 229
giraffe 310, 311, 331 *et seq.*
hippo 251, 259 *et seq.*
Hylochoerus 197
Mesochoerus 197
okapi 310, 341
pig 192 *et seq.*
Proboscidea 10
rhino, African 80
white 115, 116
Rhinoceros 81
warthog 197, 232 *et seq.*
zebra, common 170, 172, 177
Fighting, mock,
elephant 60
equid 132, 133
giant hog 228
Flehmen,
rhino, black 102
zebra, common 177
Food,
bushpig 202, 205, 208
camel 286
chevrotain 300, 304
elephant 42 *et seq.*
equid 125
giant hog 212 *et seq.*
giraffe 311, 323 *et seq.*
hippo 263, 264
Mesochoerus 196
okapi 340
Phacochoerus 214
Potamochoerus 185
rhino, black 93, 95
white 109
warthog 235 *et seq.*
zebra, common 168
Grevy's 147, 148
Food consumption,
camel 286, 287
elephant 46
equid 127
giraffe 325
hippo 261, 272
rhino, white 107, 109
ruminant 127
Food for man, 1, 2
camel 292
hippo 272
Hylochoerus 229
rhino, black 105
Food supply, 3, 4
giant hog 212
Foot,

Ceratotherium 89
elephant 14, 58
Loxodonta africana 33
Phenacodus 76
Foot pad,
camel 281
Form, influencing features,
equid 79
perissodactyl 79
rhinocerotid 79

G

Gait,
bushpig 198, 206
camel 278, 281, 282, 327
chevrotain 300, 301
elephant 14, 17, 32, 33, 63
equid 136
Equus grevyi 151
generuk 327
giraffe 311, 327, 329
Merychippus 123
okapi 311
warthog 198, 234
Genetic variability,
Ceratotherium 83
Diceros 83, 93
Gestation,
bushpig 208
camel 291
chevrotain 304
elephant 68 *et seq.*
giant hog 227
giraffe 335
hippo 275
okapi 344
rhino, black 91, 101
white 117
Tragulus javanicus 304
warthog 246
zebra, common 176
Grevy's 154
Gigantism, 4,
Ceratotherium 78
Loxodonta africana 33
atlantica 26
Gland, carpal,
bushpig 207
Gland, parotid,
camel 286
Gland, pedal,
okapi 340
Gland, pre-orbital,
giant hog 212
warthog 239
Gland, scent,
camel 288
chevrotain 297
hippo 260, 271
Gland, temporal,
elephant 61
Grazing,
camel 286
Equus grevyi 141, 155, 156
quagga 141, 168
giant hog 196, 213, 214
hippo 263, 272
Hylochoerus 188
Phacochoerus 188
rhino 84
warthog 238
zebra 140
Grooming,
giraffe 326
hippo 268, 273
horse 133, 135, 137
okapi 339
warthog 242, 243
zebra 134 *et seq.*
common 173
Grevy's 148
Grooming area,
zebra 135
Growth rate,
warthog 247, 248

H

Habitat, 3,
bushpig 201
Ceratotherium 80, 89
chevrotain 296, 299, 300, 307
Elephas 29
equid 127, 128, 139
Equus grevyi 147
quagga 147, 165, 166
giant hog 212, 217, 224
Giraffa camelopardalis peralta 322
giraffe 317 *et seq.*

hippo 250
Hylochoerus 188, 189
Loxodonta 29
africana 25 *et seq.*
cyclotis 27
Mesochoerus 196
okapi 340
Phacochoerus 189
Potamochoerus 189
proboscid 15, 18
rhino 87
black 93, 103
oriental 80
white 107 *et seq.*
Tragulus memnina 300
warthog 234 *et seq.*
Head,
Ceratotherium 82
elephant 63
giant hog 211
hippo 259, 261
Proboscidea 10
rhino, white 110
zebra 124
Hearing,
elephant 62
giant hog 216
giraffe 326
hippo 260
warthog 239
Herd composition,
camel 289
elephant 52, 53, 55
Equus grevyi 149
hippo 268
Hierarchy, 6
elephant 52 *et seq.*
giraffe 310, 327, 332
hippo 260, 266
warthog 242, 243, 247
zebra, common 172, 174
Grevy's 151
Historical representation,
elephant 31, 32, 39, 40
Home range,
bushpig 207
camel 287
Ceratotherium 89
chevrotain 301, 302
elephant 25, 40, 48 *et seq.*
giant hog 216, 217
giraffe 329
horse 131
okapi 340
rhino, black 93, 98 *et seq.*
grass 115
Tragulus memnina 301
warthog 240, 241
zebra, common 168
Grevy's 149
Homosexual mounting,
giraffe 331, 332
Horn, 4 *et seq.*
Giraffa camelopardalis 310
jumae 310
giraffe 310, 311, 333
okapi 344
rhino, black 103
white 118
Horn, accessory,
rhino, great Indian 81
Horn, nasal,
rhino, African 80 *et seq.*
Horn size,
Ceratotherium 80
rhino, oriental 80
Humerus,
elephant 14
Hump,
camel 285
Hunting by man,
bushpig 208
chevrotain 301, 304, 307
Colobus abyssinicus 67
elephant 66, 67, 72
giant hog 226
giraffe 337
hippo 269, 272
okapi 345
pig 188
rhino, black 103
white 109
zebra 67
Grevy's 160
Hybridization,
donkey 143
Equus 138
grevyi 141, 143

quagga 141
giraffe 318
horse 143
Hypodermis,
chevrotain 303
Hypsodonty,
Metridiochoerus 191
Notochoerus 191
Nyanzochoerus jaegeri 191
phacochoerine 191
Phacochoerus 190, 191

I

Ilium,
elephant 14
Imprinting,
zebra, common 178
Ivory,
elephant 36, 40, 66, 67, 73

J

Jaw,
artiodactyl 181, 182
Choeropsis liberiensis 252
elephant 18, 20 *et seq.*
hippo 251
Hippopotamus amphibius 252
gorgops 252
protamphibius 252
human 22
Hylochoerus 187
Proboscidea 8, 10
Jaw clashing, 6
hippo 251, 254, 259, 269, 271
Jaw, lower,
hippo 253 *et seq.*
Hippopotamus amphibius 251
gorgops 254
Loxondonta adaurora 21
africana 47
Merycopotamus 253
Metamynodon 254
Primelephas gomphotheroides 21
Stegotetrabelodon lybicus 21
orbus 21
schneideri 21
Jowl,
hippo 259

K

Kneeling,
warthog 234

L

Lactation,
camel 291, 292
hippo 277
warthog 246, 247
Latrine,
bushpig 208
giant hog 215, 216
Learning, 3
Leg length,
giraffe 313, 316
Lips,
Ceratotherium 84
Diceros 84
hippo 259
Limb,
elephant 14
Limb bones,
artiodactyl 181
Diceratherium 77
Equus 77
Hyracotherium 77
Miohippus 77
Phenacodus 77
rhino, black 77
Tapirus 77
Limb function,
elephant 14
Litter size,
bushpig 208
giant hog 227
warthog 246
Local names,
Ceratotherium simum 106
Diceros bicornis 92
Equus grevyi 146
quagga 163
Giraffa camelopardalis 313
Hippopotamus amphibius 256
Hylochoerus meinertzhageni 210
Loxodonta africana 31
Okapia johnstoni 339
Phacochoerus aethiopicus 230
Potamochoerus porcus 200
Locomotion (*see also* Gait)

hippo 257
rhino 85, 86
black 96
white 110
warthog 239
zebra, common 175
Longevity,
camel, 293
chevrotain 302
giraffe 337
hippo 272
okapi 344
rhino 91
black 103
white 118
warthog 248
zebra, Grevy's 160
Lungs,
Proboscidea 9

M

Mandible (*see also* Lower jaw)
Elephantidae 20 *et seq.*
Hylochoerus 195
Loxodonta adaurora 23
Proboscidea 8
Mastication (*see also* Chewing)
Ceratotherium 82
elephantid 22, 23
Hylochoerus 186
Potamochoerus 186
Maternal behaviour,
elephant 71
Mating,
bushpig 208
camel 290
chevrotain 304
elephant 69
giant hog 226
giraffe 335
hippo 268, 275
rhino 90
black 101, 102
white 117
warthog 243, 246
zebra, common 177
Grevy's 152
Matriarchy
elephant 52 *et seq.*
warthog 240
Maxilla,
Proboscidea 8, 9
Measurements
Camelus dromedarius 280
Ceratotherium simum 106
Diceros bicornis 92
Equus grevyi 146
quagga 163
Giraffa camelopardalis 313
Hyemoschus aquaticus 298
Hippopotamus amphibius 256
Hylochoerus meinertzhageni 210
Loxodonta africana 30
Okapia johnstoni 339
Phacochoerus aethiopicus 230
Potamochoerus porcus 200
Melanism,
giraffe 316
Metabolism,
hippo 261
Milk production, economics,
camel 292
Morphology,
Camelus dromedarius 280, 281, 284
Ceratotherium 84, 86
simum 106
Diceros 84, 86, 92
Equus grevyi 146, 147
quagga 120, 163
Giraffa camelopardalis tippelskirchi 312
Hyemoschus aquaticus 298
Hippopotamus amphibius 256
Hylochoerus meinertzhageni 210, 211
Loxodonta africana 30 *et seq.*
Okapia johnstoni 338
Phacochoerus aethiopicus 230
piglet 244
Potamochoerus porcus 200, 201, 206
Mortality,
camel 292
giraffe 319, 337
warthog 248
Mortality causes,
camel 292
chevrotain 307

Diceros 87, 95
elephant 66 *et seq.*
giant hog 222 *et seq.*
giraffe 322, 337
hippo 268, 269, 273
okapi 344, 345
rhino, white 117
warthog 232, 234, 243, 248
zebra, common 175, 176
Grevy's 147, 152, 154, 160
Mounting,
chevrotain 304
elephant 61
Mouth,
Ceratotherium 85
Mouth, adaptation,
Ceratotherium 84
Diceros 84
giant hog 196
Hylochoerus 198
Muscle, lateralis nasi, 9
Muscle, maxillo-labialis, 8, 9
Muscle, neucal,
elephant 12
Muscle, orbicularis oris, 9
Muscle, pterygoid,
Hylochoerus 195, 196
Mesochoerus 195
pig, primitive 195
Muscle, pyramidalis, 9
Muscle, rectus nasi, 9
Muscle, temporal,
elephant 11, 12
Loxodonta adaurora 23
warthog 197
Musculature,
bushpig 204
camel 283
chevrotain 294, 303
elephant 33
giant hog 225
giraffe 314
rhino, white 113
Musculature, head,
Diceros 84
giraffe 334
Hylochoerus 196
Musculature, jaw,
elephantid 22
hippo 259, 274
Hylochoerus 187, 196
Phacochoerus 187
Musculature, trunk,
elephant 36 *et seq.*
Proboscidea 8, 9
Muzzle,
Hylochoerus 195

N

Neck,
camel 282
giraffe 313, 316
giraffid 310
Neck fighting,
giraffe 331 *et seq.*
okapi 341
Nest,
bushpig 208
Nipples,
elephant 38
Nodding,
zebra 134
Nostril,
camel 285
Nurseries,
hippo 268

O

Occiput,
elephant 11, 12
Occipital arch,
elephant 11
Oestrus,
elephant 68, 69
equid 130
Equus grevyi 151
quagga boehmi 130
hippo 275
okapi 342
rhino 90
black 98, 101
white 117
warthog 226, 246
zebra, common 173, 177
Offence, 5
Olfactory chamber,
rhino 82
Ontogeny,

gomphothere 21
Orbit,
hippo 253
Organ of Jacobson,
elephant 62

P

Paedomorphism
Elephas falconeri 12, 26
Pair bond,
Equus quagga boehmi 130
Palate skin,
camel 290
Parasites,
bushpig 208
elephant 66
giant hog 223
hippo 273
okapi 344
rhino, black 103
white 109
warthog 249
zebra, common 178
Penis,
elephant 69
rhino 98
Phylogenetic evolution, 3, 4, 6
Phylogeny,
Camelidae 278, 279
ceratomorphs 80
elephant 19
equid 121, 128
perissodactyl 78
pig, African 185
proboscid 15, 17
rhino 82, 83
Physiology, 4
Pigment variation,
hippo 261
Placenta,
elephant 71
Placental scar
elephant 52, 53
Play, 7
equid 132, 133
giant hog 228
hippo 277
rhino, black 102
zebra, common 178
Polymorphism,
Equus caballus 139, 140
quagga boehmi 139, 140
quagga 139, 140
zebra 139
Population density, 4
bushpig 206, 207
Ceratotherium 88, 89
chevrotain 301
Diceros 88
elephant 48 *et seq.*
equid 128, 129
Equus grevyi 149, 160, 161
quagga 147, 160, 168
giant hog 212, 218, 221, 222
giraffe 311, 330
Hippopotamus 264, 268 *et seq.*
rhino, black 93, 103, 105
white 118
Population regulation, 3
bushpig 208
elephant 73 *et seq.*
hippo 268 *et seq.*
rhino 90
white 116
Posture,
elephant 63
Predation, 3, 5
Predators, 3
bushpig 208
elephant 65
giant hog 226
giraffe 337
hippo 269, 273
okapi 344
rhino 87
black 96, 103
white 107
warthog 243, 248, 249
zebra, common 175
Pregnancy,
elephant 69, 70
rhino 101
zebra, common 174
Proboscis (*see* Trunk)
Protective response (*see also* Defence)
elephant 55, 57 *et seq.*
rhino, African 101

zebra, common 174
Puberty (*see also* Sexual maturity)
elephant 71

R

Radiation,
artiodactyl 183
elephantid 20
equid 121
Equus 123, 127
Hippopotamidae 253, 254
proboscid 16 *et seq.*
suid 184, 185
ungulate 184
Radiocarbon dating, 3
Reaction to dead,
elephant 57, 58
Refuge, aquatic,
chevrotain 301
hippo 250
Reproductive efficiency, 4
equid 130
Reproductive status, 3
Respiratory tract,
elephant 38
Rhinarium,
bushpig 201
giant hog 196, 211
Hylochoerus 186, 198, 199
Mesochoerus 196
Rhinencephalon,
rhino 82
Ritual,
bushpig 193, 206
chevrotain 297
equid 132, 133
giraffe 310, 331
hippo 260, 269
Hylochoerus 195 *et seq.*
Phacochoerus 195
pig 193
Potamochoerus 195
rhino 81, 88
warthog 242
zebra, common 170, 172
Ritualization, 5, 6
Rootling,
bushpig 202, 205
Phacochoerus 188
Rumination,
artiodactyl 182
giraffe 325
periosodactyl 78, 79
Rut,
camel 290

S

Salt,
Hylochoerus 215
Scapula,
Equus asinus 143
caballus 143
grevyi 143
quagga 143
Scent marking,
bushpig 207, 208
camel 288
Ceratotherium 88
chevrotain 297
giant hog 216
hippo 262
okapi 340
rhino 88
black 98
white 110, 112
warthog 239, 240
Scenting,
elephant 62
Equus caballus 170
rhino 95
zebra, common 170
Scrape,
giant hog 216
Scratching,
rhino 88, 95
Seasonal changes, 16
warthog 243
Seasonal movements,
chevrotain 300
elephant 42 *et seq.*
giant hog 216
giraffe 329
hippo 264
rhino, black 93
white 109
warthog 235
zebra, common 168
Grevy's 149, 150

Secretion,
bushpig 207, 208
giant hog 212, 216, 227
hippo 271
Secretion, apocrine,
elephant 61, 62
Semi-domestication, 2
Sensory organ,
elephant 38
Sex ratio,
chevrotain 302
giraffe 333
hippo 277
warthog 248
Sexual dimorphism,
giant hog 211
hippo 269
Loxodonta 13
proboscid 12
warthog 232
Sexual maturity (*see also* Puberty)
bushpig 208, 209
camel 289, 292
chevrotain 306, 307
giant hog 229
giraffe 335, 337
hippo 277
rhino, black 103
white 117
warthog 248
zebra, common 172, 173
Grevy's 159
Sheltering,
chevrotain 301
giant hog 185
okapi 340
warthog 185, 188, 234 *et seq.*
zebra, common 170
Sight,
camel 285
elephant 62, 63
giant hog 216
giraffe 326
hippo 260
rhino 96, 97
warthog 239
Sinuses,
elephant 12
Hylochoerus 197
Phacochoerus 197
Potamochoerus 197
Size, 4
Elephas falconeri 12
mnaidriensis 12
namadicus 12
planifrons 12
hippo 257
Loxodonta africana 23, 25, 32, 34
Proboscidea 8, 10
rhino 84
white 107
Skeleton,
bushpig 204
camel 282
chevrotain 302
elephant 32
Equus grevyi 144
giant hog 225
giraffe 315
Hippopotamus amphibius 257
okapi 345
Phacochoerus aethiopicus 231
Skin,
chevrotain 303
hippo 260, 261, 271
pigmy 250
rhino, black 96
Skull, 4, 5
Bunolistriodon 185
bushpig 194, 201
camel 279
Ceratotherium 82
chevrotain 306
Choeropsis liberiensis 252, 253
Diceros 87
elephant 11 *et seq.*
Elephas falconeri 26
Equus 122
asinus 126
caballus 126
grevyi 126, 127
quagga 126, 147
quagga 139
sanmaniensis 127
giant hog 195
giraffe 310, 333
Gomphotherium angustidens 15
Hyemoschus aquaticus 296

hippo 250, 254
Hippopotamus amphibius 252
gorgops 252
protamphibius 252
Hylochoerus 195, 198, 199
Hyracotherium 76, 122
Loxodonta 13
adaurora 24
africana 24, 34
cyclotis 26
Merychippus (Protohippus) 122
Merychippus republicans 126
Merycopotamus dissimilis 253
Mesochoerus 186
limnetes 194
Mesohippus 122
Metridiochoerus andrewsi 192
Moeritherium 15
Notochoerus capensis 192
Nyanzachoerus tulotes 185, 192
okapi 341
Palaeochoerus 185
Perchoerus 253
Phacochoerus 191, 195
africanus 192
antiquus 192
Phenacodus primaevus 76
Phiomia minor 15
Pliohippus perix 126
Potamochoerus 191, 195
proboscid 10, 11
Protapir validus 15
Stegodon ganesa 17
Stegotetrabelodon syrticus 15
suid 197
warthog 190, 191, 245
Skull, adaptation,
artiodactyl 181
elephant 11 *et seq.*
equid 122, 123, 126
Proboscidea 10
suid 185 *et seq.*
Skull, buttressing,
Caenopus 83
Ceratotherium 82, 83
Dicerorhinus 83
Paradiceros mukiri 83
Skull, change with age,
elephantid 29
Skull, pneumatization,
elephant 11, 12
Elephas falconeri 12
hysudricus 12
mnaidriensis 12
namadicus 12
Loxodonta africana cyclotis 12
proboscid 11, 12
Sleep position,
rhino 96
Sleeping site,
giant hog 216, 217
Smell, sense of,
camel 285
elephant 61, 62
giant hog 216
giraffe 326
hippo 260
perissodactyl 82
warthog 239
Snout,
chevrotain 300
Hylochoerus 197, 198
Snout knocking,
giant hog 228
Social adaptation, 7
equid 129
Social behaviour,
bushpig 207 *et seq.*
camel 288 *et seq.*
Ceratotherium 80 *et seq.*
chevrotain 301 *et seq.*
Diceros 90, 97 *et seq.*
elephant 47 *et seq.*
equid 129 *et seq.*
giant hog 211 *et seq.*
giraffe 329 *et seq.*
hippo 262 *et seq.*
horse 139
okapi 341 *et seq.*
rhino, oriental 80
white 112 *et seq.*
warthog 240 *et seq.*
zebra 134 *et seq.*
common 170 *et seq.*
Grevy's 148 *et seq.*
Social bond,
Ceratotherium 89, 90
equid 132, 137

giant hog 216
giraffe 330, 331
rhino, black 99
white 115
zebra 134 *et seq.*
Grevy's 157, 159
Social development, 3
Socialization, 3, 4, 7
equid 135 *et seq.*
zebra 135 *et seq.*
Specialization, 2, 3
giraffe 308
Squamosal,
elephant 11
"Standing reflex,"
pig 226
Starvation,
elephant 66, 72, 73
rhino 66, 87
Stomach,
artiodactyl 182
bovid 182
camel 285, 286
camelid 182
elephant 38
Equus 78
giraffid 182
hippo 250
hippopotamid 182
suid 182
tragulid 182
ungulate 78
Strength,
rhino 81
white 110
Stripes (*see also* Coat pattern)
Equus caballus prezwalskii 131
grevyi 147
quagga 165 *et seq.*
boehmi 166
horse 131, 132, 139
zebra 131 *et seq.*
Stripes, function,
equid 135 *et seq.*
Stripes, response to,
zebra 135 *et seq.*
Submergence,
hippo 260
Submission,
elephant 61
giant hog 216
giraffe 327
hippo 262, 267, 268
rhino 81
white 112, 115, 116
warthog 242, 243
zebra 134
common 172
Grevy's 151
Sucking,
giraffe 335
hippo 277
okapi 344
Survival, 15
chevrotain 307
hippo 261
okapi 345
rhino, white 109
Swimming,
bushpig 206
chevrotain 301
Elephas 64
giraffe 325
hippo 257
Loxodonta africana 64
Symbolism,
zebra, common 179
Sympatry,
hippo 253

T

Tail,
giraffe 327, 337
hippo, 260
Taming,
zebra, common 173
Teeth (*see also* Dentition) 4, 5
Ceratotherium 78
chevrotain 297
Diceros 78
elephant 18 *et seq.*
Elephas recki 20
giraffid 308
Gomphotherium angustidens 22, 23
orbus 22, 23
hippo 251, 252
Hylochoerus 186
Hyracotherium 78

Loxodonta africana 22, 23, 25
Merycopotamus 253
Primelephas gomphotheroides 22, 23
Proboscidea 10, 16 *et seq.*
rhino 82
Stegotetrabelodon 22
suid 192
Teeth, canine, 5, 6
chevrotain 297
Notochoerus 192
warthog 197
Teeth, cheek,
elephant 18
giraffe 181
Proboscidea 10
Teeth, evolution,
elephantid 18 *et seq.*
equid 121
proboscid 16 *et seq.*
Teeth, incisor, 6
artiodactyl 181
hippo 251, 259
Proboscidea 8, 10
Teeth, molar,
artiodactyl 181
chevrotain 307
elephant 18 *et seq.*
Elephas 23
Equus 121
Hylochoerus 187
Hyracotherium 121
mammoth 23
Merychippus 121
Mesochoerus 195
Mesohippus 121
Phacochoerus 188, 190
Pliohippus 121
proboscid 16
Stegotetrabelodon 21
Teeth, molar sequence,
elephant 18, 19
Teeth, premolar,
proboscid 20
Temporal region,
elephant 12
Territory, 6
Ceratotherium 88 *et seq.*
chevrotain 304
equid 128 *et seq.*
hippo 266
rhino 81
black 98, 99
white 110, 112, 115 *et seq.*
zebra, common 177
Grevy's 148 *et seq.*
Territory, nomadic,
equid 129
zebra 129, 130
Testes,
elephant 38
warthog 243
Thermal sensitivity,
warthog 234, 246
Thermal tolerance,
chevrotain 300
giant hog 212
Thermoregulation, 4
bushpig 234
camel 285, 286
elephant 34
hippo 261
rhino, African 87
warthog 234
zebra 140
Threat,
hippo 272
Hylochoerus 198
zebra, Grevy's 157
Throat pattern,
chevrotain 299
Toes,
camel 281
hippo 250
perissodactyl 76
Tongue,
elephant 47
giraffid 308, 309
okapi 339
Tooth aberrancy,
warthog 190
Tooth crown,
elephantid 23, 25
Hylochoerus 187
proboscid 17 *et seq.*
Tooth cusp,
elephant 20 *et seq.*
Hylochoerus 186

Potamochoerus 186
Tooth succession,
elephant 19
Hylochoerus 187
warthog 245
Tooth wear,
elephant 18, 19
Hylochoerus 186, 187
Tree felling,
elephant 45
Tree-pushing,
elephant 59
Trunk, evolution,
Proboscidea 8 *et seq.*
Trunk, function, 9, 10
elephant 36, 38, 45, 46
Tush,
chevrotain 303
Tusk, 4 *et seq.*
bush pig 193
Dicerorhinus 82
elephant 10 *et seq.*
Elephas celebensis 21
planifrons 23
giant hog 193, 196, 211
Hylochoerus 193
Loxodonta adaurora 23
africana 34, 36, 53, 54
Mammuthus meridionalis 23
Metridiochoerus andrewsi 192
jacksoni 192
notochoerine 191
Notochoerus capensis 192
Nyanzochoerus tulotes 192
phacochoerine 191
Phacochoerus 190, 193
africanus 192
antiquus 192
Potamochoerus 193
Primelephas gomphotheroides 21
Stegodibeledon 21
Stegotetrabelodon lybicus 21
orbus 21
warthog 232
Tusk, evolution,
elephant 10 *et seq.*
Tusk, function, 10
elephant 45, 53, 54
suid 192, 233
Tusk, growth,
elephant 36
Phacochoerus 190
Tusk, pseudo,
warthog 242

U

Urination,
warthog 246
Urine spraying,
rhino, African 87 *et seq.*
black 98, 102
white 110

V

Variation,
proboscid 17
Vascular valves,
giraffe 311, 313
Vertebra,
Ceratotherium 86
Vertebra, atlas,
Hylochoerus 198
Phacochoerus 198
Potamochoerus 198
Vibrissae,
camel 285
elephant 62
giraffe 325
zebra, common 134
Grevy's 134, 148
Vocalization,
bushpig 206
camel 291
Ceratotherium 89
chevrotain 304
giant hog 226
giraffe 326
hippo 271
Loxodonta africana 34, 53, 62, 63
cyclotis 27
okapi 342, 344
rhino, black 97, 101
white 112
warthog 242, 246
zebra, common 170, 174
Grevy's 152

W

Wallowing, 4,
hippo 261
rhino 87
black 95
white 109, 111
warthog 239
"Warts",
warthog 232
Water circulation system,
camel 285
Water conservation,
camel 285, 286
Weaning,
camel 291
elephant 71
giraffe 335
Hyemoschus 306
okapi 344
Tragulus javanicus 304
Weight,
Camelus dromedarius 280
Ceratotherium simum 106
Diceros bicornis 92
elephant, African 14, 30
Equus grevyi 146
quagga 163
Giraffa camelopardalis 313
Hyemoschus aquaticus 298
Hippopotamus amphibius 256
Hylochoerus meinertzhageni 210
Okapia johnstoni 339
Phacochoerus aethiopicus 230
Potamochoerus porcus 200
Wool,
camel 286
Wounding, 6
hippo 268
chevrotain 302
Wrestling,
Proboscidea 9
rhino, white 112

Y

"Yawning",
hippo 251, 254, 262, 271
Young,
bushpig 208, 209
camel 291
elephant 71
equid 132
giant hog 227 *et seq.*
giraffe 318, 319, 335
Hyemoschus 304, 306
hippo 275, 277
okapi 344
rhino, black 91, 102, 103
white 117, 118
Tragulus javanicus 304
warthog 246, 247
zebra, common 178
Grevy's 159
Young, care of,
Ceratotherium 91
Diceros 91, 102
giant hog 227, 228
giraffe 335
hippo 267, 268
okapi 344
rhino, white 117
zebra, Grevy's 154
Young, conditioning,
zebra 135 *et seq.*

Z

Zygomatic process,
elephant 11

Journal of Zoology

Editor
H. Gwynne Vevers

Publication: Monthly

Subscription
Volume 187-189, 1979

The *Journal of Zoology* being the Proceedings of The Zoological Society of London which were founded in 1830, contains original papers within the general field of experimental and descriptive zoology and notices of the business transacted at the Scientific Meetings of the Society.

Published for the Zoological Society of London by Academic Press

From Recent Issues

A. S. Jayes and R. McN. Alexander: Mechanics of locomotion of dogs (*Canis familiaris*) and sheep (*Ovis aries*).

I. W. B. Thornton: White tiger genetics - further evidence.

C. A. Dixon, J. M. Erickson, D. N. Kellett and M. Rothschild: Some adaptations between *Danaus plexippus* and its food plant, with notes on *Danaus chrysippus* and *Euploea core* (Insecta: Lepidoptera).

P. T. White and I. R. F. Brown: Haematological studies on wild African elephants (*Loxodonta africana*).

J. Green, S. A. Corbet, E. Watts and O. B. Lan: Ecological studies on Indonesian lakes. The montane lakes of Bali.

P. N. Dilly and P. J. Herring: The light organ and ink sac of *Heteroteuthis dispar* (Mollusca: cephalopoda).

EAST AFRICAN MAMMALS

An Atlas of Evolution in Africa

Volume I

Reprinted in 1978 with additions and corrections.

1971, x 446pp., 0.12.408301.3

"It is something of an anatomical atlas, something of an encyclopaedia of animals, something of an anecdotal account of African wildlife and something of a text on the evolution of mammals. In total [illegible] it is a fascinating book and a staggering work of inspiration and dedication, particularly when one appreciates that every [illegible] drawing, dissection, chart or map, of which there are hundreds, is the work of the author."

J. R. Napier in **Journal of Anatomy**

Contents

I An Introduction to Method
II East African Environment
III Vegetation
Appendix I Bwamba Forest
IV Time Perspectives in Mammalian Evolution
Appendix II Anatomy of Mammals
PRIMATES
Hominoids. Man and Pre-Man. Apes. Old World monkeys. Colobus monkeys. Baboons. Mangabeys. Guenons. Prosimians. Lorises. Galagos.
HYRAXES
Anteaters
PANGOLINS
PROTOUNGULATES
SIRENIANS
Appendix III Preliminary Data Sheet. Families and approximate number of species of mammals found in East Africa. Gazeteer. Bibliography. Systematic index. Subject index.

Volume IIA

1974, xii + 392pp., 0.12.408302.1

Contents

Preface
Acknowledgements
Introduction
INSECTIVORES
Tenrecs and Potamogales. Golden moles. Hedgehogs. Elephant shrews. Shrews.
BATS
Fruit bats. Long-tongued bats. Insect bats. Sheath-tailed bats. Leaf-nosed bats. Mouse-tailed bats. Slit-faced bats. Large-winged bats. Horseshoe bats. Hipposiderid bats. Vesper bats. Molossid bats.
Bibliography. Systematic index. Subject index.

Volume IIB

1974, [illegible] + 420pp., 0.12.408342.0

Contents

HARES
RODENTS
Squirrels. Funisciurine squirrels. Sun squirrels and Giant squirrels. Ground squirrels. Anomaluroids. Anomalures. Spring hares. Mole-rats, Blesmols and Root-rats. Blesmols. Root-rats. Myomorphs. Rat-like rodents. Cricetid rodents. [illegible]bils. Crested rats. Dendromuri[illegible]. Pouched rats [illegible] mice. P[illegible]omyscine mice. Groove-toothed rats. Rats and Mice. Dormice. Hystricomorphs. Old World porcupines. Thryonomid rodents.
Gazeteer. Bibliography. Systematic index. Subject index

Volume IIIA

1977, viii + 476pp., 0.12.408303.x

Contents

Preface
CARNIVORES
Canids
Jackals and dogs
Golden jackal, common jackal. Side-striped jackal. Blackbacked jackal. African wild dog, C[illegible] hunting dog. Bat-eared fox.
Mustelids
Mustelines
Zorilla. Striped weasel. Ratel, honey badger.
Otters
Spot-necked otter. Swamp otter. African clawless otter.
Viverrids
Civets and genets
Genets. Common genet. Blotched genet. Servaline genet. Giant forest genet. African linsang. Aquatic civet. African ci[illegible]. Indian civet.
Palm civets
Palm civet.
Mongooses
Ichneumon, Egyptian mongoose. Snouted ichneumon. Slender mongoose. Dwarf mongoose. Savanna mongoose. Marsh mongoose. Banded mongoose. Long-nosed mongoose. White-tailed mongoose. Meller's mongoose. Four-toed mongoose.
Hyaenas
Spotted hyaena. Striped hyaena. Aardwolf. Proteles.
Cats
Wild [illegible]. Serval cat. Caracal. Golden cat. Leopard. Lion. Cheetah.
Gazetee[illegible] Bibliography. Systematic index. Subject index.

Academic Press

London New York San Francisco

A Subsidiary of Harcourt Brace Jovanovich, Publishers

24-28 Oval Road, London NW1, England 111 Fifth Avenue, New York, NY 10003, USA

PO Box 300, North Ryde, NSW 2113, Australia.

Printed in England

0.12.408343.9